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**PROPAGATION AND MIGRATION
OF FOUR SPECIES OF STERNA**

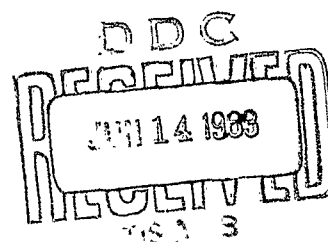
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PROPAGATION AND MIGRATION OF FOUR SPECIES OF STERNA

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PROPAGATION AND MIGRATION OF FOUR SPECIES OF STERNA

by

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Introduction

Within the family Sterna, there are several species which appear to be closely related to each other at first sight. These species are *S. hirundo* and *S. macrura* in the Northern Hemisphere and *S. hirundineacea* and *S. vittata* in the Southern Hemisphere. These species have interesting particularities in regard to distribution and migration. This report is intended to give a summarizing description on the distribution and migration of species of Sterna based on data from the more important handbooks of fauna and animal-geography. At the same time, it will contain also accounts on the ecology of the different species. Secondly, an attempt will be made to explain, from ecological and historical conditions, their present-day distribution and the present-day paths of migration as far as the latter are known with a certain degree of accuracy. In conclusion, the taxonomic position of the species will be discussed. It is probable that gaps exist in regard to our knowledge of distribution and migration. This is explained to a great extent by the difficulty of obtaining and processing Russian literature. The investigations on bird migration carried out intensively especially in the Nordic countries, in the Baltic Area, in Central Europe, in Great Britain and in the United States, have produced in many cases results which can now be used also for purely theoretical discussions.

The hydrological maps are based on Schott 1926 and 1935 whereas the climatological indications are derived from Schott-Bonnier World Atlas and from Hettner 1930 and 1932. The maps of distribution have been prepared from data procured from a number of communications listed under literature references. In regard to the distribution of *S. hirundo* and

S. macrura in the Nordic countries. I base myself on indications in some Nordic Journals (Note: For indications on the nutrition of *Sterna macrura* and *S. hirundo*, I am indebted to Kjell Kolthoff, Lars Faxen and Tage Borch in Upsala and, for indications on the distribution of *S. macrura* in Siberia, to Dr. H. Johansen in Copenhagen.).

I. Special Section

Sterna hirundo Linné

Characteristics: The difficulty of distinguishing *S. hirundo* and *S. macrura* in nature is generally known and attested in literature. In their winter and young-bird plumage, the two species are very difficult to distinguish. Witherby states in regard to *S. macrura*: "In their winter and immature plumage, distinguishable only under the most favorable conditions from *S. hirundo*." Only during the breeding period can the two species be distinguished in nature with a considerable degree of accuracy. However, it is then necessary to come as close as possible to the sea swallows and observe them with a good pair of binoculars. It is generally stated that *S. hirundo* is distinguished from *S. macrura* by having a black-tipped bill whereas the latter are supposed to have a wholly red bill. These characteristics as a rule offer good differentiation but it does happen that, during the breeding period, *S. hirundo* also has a wholly red bill and *S. macrura* one with a black tip. However, in regard to the red pigmentation, there always seems to exist a difference of nuance in the two species. The color of the bill of *S. hirundo* slightly shades into yellowish-red whereas that of *S. macrura* is strongly blood red. On dried skins, stored in the dark, of the two species of sea swallows, this difference in the basic pigmentation of the bill can still be observed. When the birds sit, another satisfactory differentiation also consists in the different length of the tarsi of the two species. *S. macrura* has very obviously shorter tarsi than *S. hirundo*. Niethammer (1942) says in regard to *S. macrura*: "Stride very short so that the feet can be barely seen in the sitting bird." In all of the skins examined by me, a perceptible difference could be noted. Hortling (1929) indicates the length of the tarsus of *S. macrura* as 14-17 mm and of *S. hirundo* as 19-21 mm.

Witherby states in regard to the last named characteristic the following: "If settled in positions where extremely short legs can be clearly seen, this affords a reliable distinction (in regard to *S. macrura*) at all seasons for observers sufficiently familiar with the common tern which stands quite noticeably higher off of the ground."

In the mating plumage, there is a further difference in the color of the lower part of the body which generally shades perceptibly more strongly towards gray in *S. macrura* than in *S. hirundo* and the gray color generally extends very perceptibly as far as the under-throat, bridle and the region of the ears.

We might also mention that the inner vane of the first wing-end feather has a broader dark streak in *S. hirundo* than in *S. macrura*. However, the width of the streak seems to vary greatly so that this characteristic can in certain cases be utilized for differentiation only with difficulty. Witherby warning against utilizing the length of the tail as a characteristic of differentiation is probably justifiably.

According to Witherby, there is no constant difference between the young in the nests of *S. hirundo* and *S. macrura*.

General Distribution: *S. hirundo* (fig. 1) is found in the Northern Hemisphere in general between the Polar Circle and the Tropic of Cancer. It occurs along the coast as well as on inland water courses. In the Old World, it goes beyond the Polar Circle on the Scandinavian Peninsula and can be found along the Norwegian coast as far as Eastern "Finnmarken". Olsen (1921) writes in regard to its occurrence in Norway: "breeds generally along the coast beyond the Lofotens; North of this region, it is occasionally found as far as Eastern "Finnmarken" (Orig. norweg.). The Northern-most find of the species was from the North Cape but it does not exist in the Faroe Islands and Iceland, according to Hartert. In the Northern and Eastern parts of Asiatic Russia, *S. hirundo* is found along the middle Ob, along the upper Ienessei, the Upper Tunguska and around Lake Baikal. It also occurs along the Eastern coast of Asia. According to Bergman (1935), the species *longipennis* Nordmann breeds on Kamtschatka. Hartert reports that *S. hirundo longipennis* occurs on Kamtschatka, in Manchuria, around Lake Baikal, in the Delta of the Lena as well as on the coast east of the latter. If this is correct, *S. hirundo* would therefore at the latter point also go beyond the Polar Circle towards North. In Central and Eastern Asia, the species is not represented by the type *S. h. hirundo* which is the only one considered in this report. Witherby mentions the following Asiatic sub-species: *Tibetana* (Tibet, Turkestan), *longipennis* (Northeastern Asia), *turkestanica* (Western Turkestan) and *minussensis* (Altai); "...but their distinctions seemed doubtful." Stegmann (1938) gives no information on *S. hirundo* either in the Arctic or in the Siberian or Chinese regions of fauna so that we will have to consider the indications on the occurrence of the species in Northeastern Asia as not confirmed. *S. h. longipennis* is listed by Alexander (1928) as an independent species occurring in Northeastern and Eastern Asia: "breeds on the coast and lakes of" It appears to me that the separation of type as species is well founded.

In the South, *S. hirundo* extends as far as Mesopotamia, the coast of the Persian Gulf, and the coast of North Africa. The species is also found on the Azores, in Madeira and the Canary Islands.

In North America, the occurrence of *S. hirundo* extends from the region of the Great Slave Lake, the South coast of the Hudson Bay and the Southern Ungava region on the North as far as the coast of the Gulf of Mexico in the South. The area of distribution covers the Eastern half of

North America but the species does not appear to breed West of Saskatchewan, North Dakota and Texas. In North America, *S. hirundo* apparently does not extend as far as the Polar Circle, in the South, it occurs almost as far as the tropics like in Asia. Murphy (1936) does not list the species as one breeding in the Caribbean Sea and doubts that it breeds along the coast of Venezuela. However, Witherby mentions *S. hirundo* as a bird breeding in the Dutch West Indies and along the coast of Venezuela. Murphy says: "since it is doubtful whether the common tern nests anywhere within the South American region, I have omitted the description of the eggs and the youngest stages."

Distribution in Nordic Countries: *S. hirundo* is found in general on all the coasts of Sweden. The distribution of the species along the coast of Norway has already been mentioned. According to Olsen, it breeds in Norway occasionally also along small water courses in the interior of the country but only exceptionally on those far distant from the sea, in Southern Sweden, the occurrence of the species is customary along the water courses of the inland as far North as Värmland, Närke, Västmanland and Uppland. It is also found along the two Deil Lakes as well as on the Siljan and Jämtlands Storsjö lakes but is otherwise absent or infrequent in norrländic waters and is also absent from the Northern Finnish water courses.

Hibernation Area and Migration: According to Niethammer, the European river sea swallows appear to hibernate primarily along the coast of Africa from Senegambia as far as the Cape. Hibernation also takes place in Madagascar, on the coasts of Upper and Lower India, on the Malacca Peninsula and on the coasts of China. According to Hartert, *S. h. longipennis* winters as far as the Louisiade Archipelago. According to Murphy, *S. hirundo* winters in America from Florida and the coast of Mexico south along the coast of the Caribbean Sea, extends along the West coast of South America as far as Ecuador and on the East coast as far as the Straits of Magellan and is also found on the Falkland Islands during the winter of the Northern Hemisphere.

The Nordic, Baltic and Western European contingents of *S. hirundo* migrate along the west coast of Europe. Sea swallows from Switzerland were found in South and Southwest France, according to Niethammer. The same author further reports that birds from Sweden, Finland, Denmark, Germany and the Netherlands were found to winter along the tropical West and Southwest coast of Africa. A bird ringed in Sweden was found in Kapstadt.

S. hirundo returns late to the breeding areas and leaves them early. It arrives in Germany towards the end of April and the beginning of May but migrating birds can be observed until the end of May (Niethammer). The birds from England return to the South coast of England after the middle of April but some have been observed at the beginning of February. Most of them arrive in the last week of April (Witherby).

S. hirundo arrives in Central Sweden in early and middle May. We might say with the natives of Uppland (Central Sweden) that the river sea swallow returns at the same time as the cuckoo (cf. Wright).

In Germany, *S. hirundo* begins to migrate from the breeding areas already in July. Departure takes place mainly from the end of July to the end of September. According to Niethammer, occasional birds may remain as late as the beginning of November. Departure from England is begun after the middle of July and terminated by the end of August. In Sweden, according to Lönnerberg (1935), *S. hirundo* appears to depart westward already at the beginning of July. From Southern and Central Sweden, *S. hirundo* generally leaves towards the middle of August.

Hartert stresses that occasional birds not infrequently remain in the tropics during the summer of the Northern Hemisphere but do not there breed. Olsen (1921) mentions that some birds have also been seen around Kapstadt during the Northern summer.

Food Supply: Literature contains a number of data on the food supply of *S. hirundo* and also studies on the stomach content of the river sea swallows (cf. Niethammer). An English report gives the following stomach content: 40.32% fish, 19.09% insects and the remainder crustaceans and "sea worms." The fish caught by *S. hirundo* belong to several groups of which a preferred kind is *Ammodytes* but there are also listed the young of *Anguilla*, *Pleuronectes*, *Rhombus*, *Clupea*, *Engraulis* and *Gobius*. It is reported from the mouth of the Elbe that *S. hirundo* aggregates here during the late summer to catch the young of *Osmerus eperlanus*. Wright mentions that *S. hirundo* catches small "strömlings," sand eels and "Sticklings" (Note: Kolthoff states in a letter that the young like to feed on such insects as *Galeruca nymphae* and *Donacia*. Adult birds occasionally also catch such insects as *Trichopterae*). Olsen writes that *S. hirundo* can be found in Norway almost exclusively along the coasts and feeds on "small fishes and in part also on crabs (e.g., *Idotheae*) (in Norwegian original). Forbush (1936) states that the species feeds in North America "on small fry, shrimps and other small crustaceae but occasionally also on grasshoppers and many flying insects."

It would therefore seem as if the species within its entire distribution or breeding areas feeds mainly on the young of different kinds of fish which live under such conditions that the sea swallow with its methods of catching can obtain them. Insects and crustaceans appear to constitute a not inconsiderable share of the bill of fare of *S. hirundo*. Among the latter, Niethammer mentions Leander and Crangon. Especially inland, *S. hirundo* catches, as stressed by Niethammer, quite a variety of insects and will hunt flying mosquitos. *Coleoptera* and dragon flies may also serve as food.

Sterna macrura Naumann (coastal sea swallow)

General Distribution: The breeding area of *S. hirundo* coincides quite well with the so-called temperate zone, defined in the North by the

+10°C isotherm of the warmest month and in the South by the +20°C isotherm of the coldest month (cf. Schott 1926). The area of distribution of *S. macrura* is located North of that of *S. hirundo* although the southern and northern parts of the areas of the respective species overlap somewhat at certain points and quite appreciably in Northwestern Europe. Consequently, *S. macrura* mainly breeds within the climatologically arctic region where the southern limit consists of the +10°C isotherm of the warmest month. Along the West coast of Europe and along both the West as well as the East coasts of North America, however, the area of distribution of *S. macrura* extends far to the South of the borderline mentioned. In Europe, *S. macrura* is found southward as far as Ireland, Middle England, Scotland, Holland and Denmark (Hartert). Witherby stresses the prevaillingly maritime character in the distribution of *S. macrura* different from that of *S. hirundo* but also reports that *S. macrura* breeds in some inland water courses of Ireland and Northern Scotland. During the migration periods, it is observed in the British Isles as well as elsewhere more frequently along the water courses of the inland. Witherby reports that *S. macrura* is more numerous along the West coast of Scotland and Ireland as well as in the Shetland and Orkney Islands than *S. hirundo*. It is also the "chief breeding species" in the Hebrides.

According to Lincoln (1935), *S. macrura* in North America can be found breeding along the east coast southwards as far as Massachusetts (as far as Nova Scotia according to Taverner, 1934) inland as far as Hudson Bay and the Great Slave Lake. On the west coast of North America, the species is found as far as Northern British Columbia.

Towards the North, *S. macrura* breeds within the arctic region as far within the North Pole region as it is able to find suitable nesting places (Lincoln 1935). It was found to breed only 7°30' from the North Pole.

The breeding area of *S. macrura* is around the Pole. Concerning Eurasia, Stegmann (1938) designates *S. macrura* as arctic and lists it among the 45 bird species which he regards as purely endemic for the arctic region around the pole which he equates with the "Palearctic." Within Asia, the species breeds almost only within the Arctic and extends the furthest southward along the lower courses of the Siberian rivers flowing North. If we consider the present distribution of *S. macrura* over the entire Northern Hemisphere, it seems to us correct to designate the species as arctic-boreal (Stegmann). Spärck (1942) designates *S. macrura* as arctic-boreal and inclines to the opinion that it was one of the first birds which took possession of the coast of the "Yoldia Sea." Ekman (1922) groups *S. macrura* in Northern Europe among the sub-arctic species of Northeastern origin. In view also of the occurrence of *S. macrura* within the cold-temperate zone (boreal), it can be stated that it is most numerous in Northwestern Europe in the sub-arctic or boreal-arctic regions (according to the definition of Appellöf, 1905) and in those parts of the boreal region bordering closely on this sub-arctic region of

transition (cf. Ekman 1935). Olsen (1921) writes that the largest colonies of *S. macrura* are in "Finnmarken". According to Niethammer, in Germany the species is most numerous along the northernmost part of the coast, the North-Frisian Islands. That *S. macrura* which is a pronounced coastal bird, is most numerous within the sub-arctic and arctic coastal regions can be concluded also from the fact that it is most numerous also around the lakes and along the rivers within these coasts. Ekman (1922) stresses that migration from the main areas of occurrence (coasts) "on the basis of customary laws of probability" (in Swedish original) generally must take place from the regions where the greatest number of birds occurs. Such migration is obviously based on ecological factors and we may suspect that competition for food and nesting places are important factors of this kind.

Distribution in Nordic Countries: We have already briefly touched on the distribution of the species in Nordic countries (fig. 4). Because it is difficult to distinguish between the eggs, the young and the adults of *S. macrura* and *S. hirundo* in nature, the distribution of the first named species as a breeder is probably known only incompletely. *S. macrura* is found at certain points of the Western and Southern coasts of Sweden (cf. map). Along the Baltic-Sea coast of Sweden, it is more frequent and is found to breed in the North on the islands of Norrbotten. On the Finnish side, the species breeds along the northern coast of the Gulf of Bothnia. In Finland, the species appears at certain points along the coast and around Lake Ladoga in adjacent Russia. It also occurs along the coast of Estonia.

On the west coast of Norway, the species is found as far as the region of Bergen but becomes numerous only north of the Trondheim Fjord and breeds most frequently in "Finnmarken," according to Ekman (1922). In Norway, north of the Lofoten Islands, *S. macrura* seems to prefer the exterior parts of the fjords and *S. hirundo* their interior parts. In Sweden, *S. macrura* breeds from the region of Jämtland Storsjö northward along sweet water. Along the water courses of the coniferous and beech regions in northern Scandinavia, the species has become distributed from the coasts of the Atlantic and the Arctic Ocean.

According to Hansch (1905), *S. macrura* breeds customarily in Iceland and can also be found in great numbers on Spitzbergen. Dinesen (1926) mentions the species as habituated to the northern coast of Iceland. According to the same author, it is also found on all the coasts of Greenland and on Barents Island ("Baren Insel"). Hartert mentions the occurrence of this species on Franz Josef Land, Ireland, Greenland, and the Faroe, Shetland and Orkney Islands. Witherby states that *S. macrura* occurs on Jan Mayen Island.

Wintering Area and Migrations: The first knowledge on the wintering areas of *S. macrura* probably goes back to the observations from the trips of the Gauss and the Valdiva in the Antarctic. Van Höfflin (1901)

and Reichenow (1904-a) furnished ornithological reports of these trips. The former mentions that the expedition found *S. macrura* southward as far as Wilkes Land. Reichenow (1904-b) also described a subspecies of *S. macrura* (*S. m. antistropha*) which is indigent along the coast of the Antarctic in his opinion. According to Murphy, it is most probable that this is not a subspecies of *S. macrura* but is *S. vittata* which is indigent along the coast of the Antarctic. Murphy (1936) is of the opinion that a great part of the southern finds of *S. macrura* should really be ascribed to *S. vittata*. During the Scotia expedition, however, *S. macrura* was observed and collected in the Weddell Sea during the southern summer and two birds were caught at 66° southern latitude outside of the Ross Sea. Along the west coast of South America, *S. macrura* was found during the southern summer in migration southward and, according to Murphy, a considerable number was collected in the region of Valparaiso. The species was also observed along the Atlantic coast of South America. Murphy mentions an observation of several hundred of the species migrating southward beyond the mouth of the Rio de la Plata. The opinion held until recently that *S. macrura* winters principally along the coast of the Antarctic probably originated with the German authors mentioned above as well as from Cooke (1911). Murphy makes a considerable attempt to counter the "legend" of the hibernation of *S. macrura* on the basis that the species has been confused with *S. vittata*. Although relatively few birds have been collected outside of the coast of the Antarctic, there do exist some definite finds. Especially because it is so difficult to distinguish between *S. macrura* and *S. vittata* in nature, it is at present impossible to decide to what extent *S. macrura* migrates south beyond the Antarctic Circle for hibernation. Other than along the coasts of the Antarctic, *S. macrura* winters along the coast of Southern Chile and Southern Argentina, according to Murphy. It also hibernates along the coasts of Southwest Africa and of the Cape Colony (cf. Niethammer). Here we should keep in mind that birds from North America were also found in West and South Africa (Lincoln, 1935). One bird was found during the southern summer on New Zealand at the mouth of the Waikanae River (Oliver, 1930).

S. macrura winters apparently within an area of the Southern Hemisphere which corresponds to its breeding area in the Northern Hemisphere from climatological viewpoints. Wintering takes place principally in the area characterized by arctic and antarctic waters which are limited by Murphy toward North from the subtropic seawater by the +15°C isotherm (according to Murphy actually the +14.5°C isotherm of the surface water during the southern summer). The same or a slightly higher temperature also characterizes the surface water on the southwest coast of Africa (cf. maps).

In consideration of the extent of the wintering area, *S. macrura* also may be designated as an arctic-boreal species. The breeding area and possibly also the wintering area are circumpolar. Proofs for the circumpolar character of the wintering area are not yet very strong; one finding

on New Zealand, two beyond the Ross Sea (66° South by 157° West) and the others during the southern summer on the coasts of South America as well as in the Weddell Sea and around the island groups in this part of the Antarctic. Lincoln (1935) indicates on his map six points where the species was found during the southern summer. Two of these points are beyond the mouth of the Rio de la Plata, one is north of southern Georgia (Fig. 3) and three are along the coast of Kronprinzessin Martha Land (Antarctic continent). *S. macrura* was not found in China (David and Oustalet, 1877), French Indochina (Delacour and Jabouille, 1931) or British India (Baker, 1929, 1930). The species is also not mentioned for Tasmania (Lord, 1924). Alexander (1928) states the following on the migratory paths of the species: "On migration it appears to keep to the oceans and is not found in southern Asia or in the Indian and the Western Pacific Oceans." It is important to remember that *S. macrura*, during the southern summer, was found mainly within the antarctic and subantarctic surface-water zone as well as within the south African cold-water zone.

For a long time the migratory paths of *S. macrura* were not definitely known. COOKE (1915) knew nothing of them. The European birds fly along the west coast of Europe and Africa (Niethammer). However, the migratory paths of the North American birds were unknown for a long time. It was known that migration did take place along the west coasts of the American continents. Birds were observed far to the South of the breeding area along the coast of California. Some few individuals have been observed, according to Cooke (1915), on the east coast of North America as far south as Long Island but not beyond this point. Austin (1928) and Wynne-Edwards (1935) have added important facts in regard to the migratory paths of the North American contingents. Birds ringed in North America have also furnished very important indications. Along latitude 51° in the Atlantic Ocean, Austin observed and collected birds during the second half of August and was able to note that North American birds migrating to their wintering area fly first East across the northern Atlantic Ocean to European waters before they turn South. During a trip across the Atlantic Ocean (as observer), Wynne-Edwards was able to observe the migration of *S. macrura* from North America to the coast of Europe during the months of August and September. Austin was able to check the migration of three North American birds which he had ringed himself. One had been ringed in Maine and was found dead in the Niger Delta four years later. The other two birds had been ringed in Labrador and one of them was found in the same year near La Rochelle in France whereas the other was found one year later in the Natal. The last one of the birds from Labrador therefore covered, from the nesting place where it had been ringed, to Natal about 9,000 miles and did so in a time which cannot have been longer than three months because it was found in South Africa on the 14th of November.

Based on the available facts on migration of *S. macrura*, we may now consider the knowledge of the migratory paths of the species as satisfactory (cf. Fig. 3). The path of the birds (Lönnerberg 1935). *S. macrura*

therefore migrates from the nordic countries and the Baltic area along the west coasts of Europe and Africa southward as far as South and Southwest Africa. Some birds from nordic countries probably also migrate by way of the British Isles. Whether birds from nordic or northwest European countries have demonstrably gone as far as the Antarctic continent, I do not know. From eastern and northern North America as well as from the Arctic Islands and Greenland, *S. macrura* migrates during late summer and fall first to the west coast of Europe. Migration from the northeastern coast of the United States first is directed northeastward as far as Nova Scotia and Newfoundland. In these areas is a junction of migratory paths from the North and Northwest. The path of migration then apparently initially goes over cold water North of the Gulf Stream but the latter is crossed by the birds where it begins to enter the Atlantic current and the birds now direct themselves toward the coasts of England and France. After the birds from North America have reached these regions, they subsequently adopt the same path South as the European birds. According to Lincoln, there is also a migratory path which leads from the Davis Straits over Iceland to western Europe. This path is probably adopted by those birds which breed in the Arctic regions of North America. Those birds from North America which do not remain in South and Southwest Africa migrate further South and Southwest to areas with subantarctic and antarctic surface waters and, in any event, as far as the Antarctic coasts. At about the same latitude with South Georgia and the Southern Sandwich Islands as well as the waters slightly north of these islands, certain contingents seem to turn northwest and have been found beyond the mouth of the Rio de la Plata (Lincoln). Other birds continue further south. Beyond the mouth of the Rio de la Plata, however, there also connects a migratory path which starts from the main migratory path along the West Coast of Africa and leads across the narrowest part of the Atlantic Ocean to the northeastern edge of Brasil (Lincoln). It would seem that this migratory path is not greatly utilized. Upon reaching the Brazilian coast, the birds continue further south and must gradually join up with the birds which have come from South Africa. Beyond the mouth of the Rio de la Plata, it therefore seems that there is a meeting area for different contingents of *S. macrura*. Further North than these waters, there are probably no birds which winter here. As a capable flier, *S. macrura* probably traverses large areas of the surface-water zones mentioned above during the southern summer.

According to Lincoln, *S. macrura* breeding in northwestern North America probably migrates along the west coast of North America. It would seem as if the birds from the coasts of the Bering Straits and the Bering Sea take the same path because I know of no other migratory paths along the east coast of Asia. In the region of the southern tip of South America, birds from the Atlantic and the Pacific Ocean must encounter each other during the southern summer. How many of the birds of the North American breeding area select the migratory path in one or the other direction does not seem to be known. On the assumption that the Atlantic migratory paths are more greatly utilized, we may suspect that a rather large part of the birds of the North American breeding area flies first East over the Atlantic Ocean before adapting a southern course.

A number of finds have been made which may possibly give some information on the migratory paths of the birds from Siberia. Hortlind (1929) mentions that *S. macrura* is "a familiar transient at Tobolsk" (in Swedish original) which lies at the confluence of the Irtych and Tobol Rivers. Figure 3 indicates that *S. macrura* occurs from the lower Ob as far as the confluence with the Irtych. According to Witherby, the species has been encountered occasionally on the Black Sea and Arrigoni Degli Oddi (1929) reports from Italy of a chance find. He stresses the difficulty of distinguishing the species from *S. hirundo*. It probably occurs more frequently in the Mediterranean than the Italian finds let us assume. The finds were made near Syracuse, Pisa, Genoa, Nice and in the Po Delta. Since *S. macrura* has not been encountered on the coast of the western Pacific or the Indian Ocean, the birds from Siberia "familiar" in Tobolsk do not spend the winter in these oceans or fly over them. It is more probable that the birds encountered along the Black Sea and at least a part of the birds observed in the Mediterranean are *S. macrura* during migration from Siberia. The migratory path at least for certain contingents of *S. macrura* from Siberia would therefore lead from the Ob, Irtych and Tobol over the Caspian and Black Sea to the Mediterranean from where the birds probably migrate south, together with the birds from North America and Europe, along the west coast of Africa. Although this hypothesis is not supported by finds of ringed birds, I feel justified in establishing it by taking into consideration the observations of migrating birds of the species which have allegedly been made at Tobolsk, along the Black Sea and the Mediterranean. Because migrating birds have never been observed along the west coast of the Pacific or the coast of the Indian Ocean, the outlined migratory path of the West Siberian populations is the most probable from ecological viewpoints unless migration also takes place along the polar sea coasts to Scandinavia and further south. That migration passes across the continent over Tobolsk does not seem to be proved but there is a large probability that North Russian and West Siberian birds normally migrate along the polar sea coast (Note: Prof. H. Johansen and Dr. A. Tugarinov state in a letter that documented observations of *S. macrura* in the Kirgizian steppes and at Tobolsk are absent and believe migration across the former to be improbable). The East Siberian birds migrate along the West Coast of America (cf. Heptner 1936, Tugarinov 1929). The map, prepared by Tugarinov, on the main migratory directions within Northern Asia and Russia makes it somewhat possible that *S. macrura* migrates from the Ob region across the Caspian and the Black Sea because, according to these indications, an important migratory path leads precisely from the region of the Ob across the areas mentioned to the Mediterranean (Fig. 5). This migratory path of the sea swallows and other aquatic birds perhaps originated during a Pluvial Age with different hydrographic conditions in Western Siberia and Turan than those of today. We might then imagine that certain populations or strains have retained this path in their memory and have transmitted it from generation to generation up to the present. It is possible that this migratory path of *S. macrura* is becoming gradually less utilized under present climatic conditions. Tugarinov also communicates that main migratory paths lead from the coastal areas of western Siberia westward along

the polar sea coast and others from the coastal areas of Northeastern Siberia eastward to the West and South coast of Alaska. According to Heptner, *S. macrura* migrates from Alaska along the West coast of North America but also eastward to the Atlantic coast and then further (Fig. 3).

We might add that, according to Witherby, *S. macrura* has been found during migration occasionally in the Hawaiian Islands.

Return migration to the breeding areas appears to follow the same paths as migration to the wintering areas. Of all birds, *S. macrura* may possibly have the longest distance of migration. The distance between the northernmost breeding areas in America and the Antarctic region amounts to about 17,600 km and at least some contingents of the species therefore annually cover a distance of travel which is twice as long.

According to Witherby and other authors, chance wintering (transit?) takes place in the European Inland or along the Mediterranean and in the States of the interior of North America. Hortling (1929) writes that hibernation can take place along the west coast of Europe. Migrating birds have been found in the inland of Germany but they were in most cases exhausted or dead birds, according to Niethammer.

S. macrura arrives in Southern Sweden from the wintering areas about simultaneously with *S. hirundo* or else at the beginning and middle of May (Wright) (Note: *S. macrura* arrives in Öland later than *S. hirundo*, as stated by Klothoff in a letter). The species has arrived in the Muonio Valley already around 20 May. In Denmark, *S. macrura* and *S. hirundo* arrive around 1 May (Salomonsen 1940). *S. macrura* returns to the German breeding areas at the end of April and the beginning of May but, according to Niethammer, birds flying northward have been observed after the end of May. According to Hantzsch (1905), *S. macrura* arrives in Iceland at the end of May but was observed at Reykjavik in one case already on 5 May. According to Dinesen, the species arrives on 11 May in Northern Iceland. In England (Witherby), *S. macrura* arrives at the end of April but there are some observations on arrivals in the first half of April. Transient birds can be observed up to the first week in June. The species arrives at the northern breeding places in America by the middle of June (Cooke 1915) and begins to leave Sweden already towards the middle and end of July (Lönnerberg 1935). According to Salomonsen, it begins to leave Denmark in August. According to Hantzsch (1905), the species disappears from the Icelandic coast at the end of August and the beginning of September. It seems as if the young of the same year are the first to migrate (Niethammer). Departure from Germany begins at the middle or end of July. Niethammer stresses that non-breeding individuals arrive as late as June in German coastal waters and leave again already in the middle of July. In general, the old birds probably do not leave Germany prior to September or October. Similar to *S. hirundo*, the species congregates during the migration period in Germany at the mouth of rivers during late

summer and fall. According to Witherby, the departure of *S. macrura* from England begins towards the end of July and by the end of August the breeding places are abandoned. Birds flying southward over English regions can still be observed in October.

Niethammer writes that *S. macrura* can be found in the Cape Colony from November into April. It would appear as if *S. macrura* may also remain occasionally in southern regions during the northern summer.

Food Supply: According to Wright, in the Baltic Sea small *Clupea harengus* membras and especially *Gasterosteus* form the habitual feed of *S. macrura*. Dirckson (1932) states that *S. macrura* catches, in addition to *Clupea* and *Anguilla*, "*Carcinus maenas* when they have just shed their exoskeleton," *Crangon vulgaris* and especially *Arenicola marina*. Witherby reports that there are few observations on the food supply of the species in the British Isles. In Arctic regions, *S. macrura* nourishes itself principally, according to the same author, from Pelagic crustaceans (*Hippolyte*, *Thysanoessa*, *Mysis*) but also of "small fish," pelagic mollusks (*Clio*, *Limacina*) and from sweet water crustaceans (*Lepidureus*). During the expedition of the Vega, *S. macrura* was observed catching "*Idothea entomon*, *Gammarus* and *Onesimus* in small puddles along sandy sea beaches" (in Swedish original) (Palmen 1887). However, Olsen inclines to the opinion that the species lives in Norway mainly from "small fishes" (in the Norwegian original). As has been mentioned, *S. macrura* can also catch insects at given times; for example, Hantzsch and Olsen state that it catches mosquitos in the air, on the ground and on the surface of the water. Hantzsch observed in Iceland that the very young are fed especially with insects and later with small fishes. In Northern Finland, *S. macrura* was observed while catching perclides.

The experienced Swedish sweet-water biologist Tage Borgh informed me verbally that *S. macrura* at the Ännsee (Western Jämtland) during the swarming period of *Sphemera vulgata* is completely dependent on the latter as food source. The species has never been observed to plunge for food at the Ännsee. There are hardly any fishes of suitable size and occurrence which could serve as food for *S. macrura*. (Note: Faxen stated verbally that *S. macrura* occasionally catches *Phoxinus phoxinus* and that Tricoptera are its main food during certain periods at the Ännsee. Kolthoff reports from Öland that *S. macrura* feeds primarily on insects (*Carabides*, the larvae of *Eristalis*, etc.).) We must therefore assume that in these waters *S. macrura* is primarily insectophage. The abundant occurrence of certain insects in sub-Arctic (high-boreal) waters can be perhaps construed as a contributory cause for the occurrence of the species along sweet water within this area. The preference of the species for insects and small pelagic crustaceans possibly has a certain connection from the point of view of the physiology of nutrition. The diet of arthropods may perhaps be derived from a principal insect diet predominating in earlier states of phylogenesis.

Judging on the basis of the available data in literature, *S. macrura* consumes more pelagic food than *S. hirundo*. In contrast to the latter, the former seems to prefer arthropods. Although there are apparently no completely comparable indications on the food preferences of the two species, it does seem apparent that crustaceans and mollusks of pelagic species occupy a considerably larger share of the bill of fare of *S. macrura* than that of *S. hirundo*. It would seem as if, among fishes, species of *Clupea* (fry) constitute the most frequent food of *S. macrura*. Along the coast, *Gasterosteus* is perhaps equally important. In regard to food, *S. macrura* also differs from *S. dougalli* Mont. which consumes only fish, according to Witherby and Niethammer.

Sterna hirundinacea Lesson (South American sea swallow)

S. hirundinacea is apparently closely related to *S. hirundo* (cf. Murphy p.1094). The former is slightly larger than the latter. Tarsi and feet of *S. hirundinacea* are stronger and the bill is also perceptibly longer and stronger. The mating plumages of both species are very similar to each other. However, *S. hirundinacea* possesses a uniform yellowish-red bill which has a darker red in the winter plumage.

Distribution: *S. hirundinacea* is restricted to the coast of the South American continent and the Islands in the vicinity of the latter. They occur furthest from the continent on the Falkland Islands. The species occupies a very extensive area which reaches from the coast of Central Peru southwards around Cape Horn and Tierra del Fuego and then further northward as far as Cape Frio on the Brazilian coast northeast of Rio de Janeiro. The northernmost breeding areas in Peru and Brazil are not definitely known, according to Murphy, but we do know that the species breeds on the San Gallan Islands on the Peruvian Coast and in the region of Cape Frio in Brazil. According to Murphy, the migrating species has been encountered on the East coast as far as Bahia and on the West coast as far as Northern Peru. It was not observed to breed in these regions. Murphy stresses that, of all the species of *Sterna* strictly restricted to the South American continent, *S. hirundinacea* has the most extensive distribution. It does not appear to have been classified into races. Murphy is of the opinion that *S. hirundinacea* is typically sub-Antarctic and stresses that it would most certainly have been assigned to the species which are restricted to the surface-water zone mentioned if its breeding area had not extended so far into tropical regions. Its particular distribution brings it about that it can be regarded to a certain extent as a "zoneless" bird. A similar and even more particular distribution is shown by *Larus dominicanus* which occurs southward in Antarctic surface-water areas and northward as far as Rio de Janeiro and Northern Peru.

It would therefore seem as if *S. hirundinacea* was not a real migratory bird to any large extent. However, more detailed indications by Murphy on this biological characteristic of *S. hirundinacea* are lacking but he does write that it is numerous in the Humboldt current region throughout the entire year.

According to the author quoted, *S. hirundinacea* extends so far into tropical regions because there exists here cold-water currents and a belt of ascending cold water. In the southernmost part of the area of distribution, *S. hirundinacea* breeds during the spring of the Southern Hemisphere but in June in Central Peru, i.e., during mid-winter. The same habits are also shown by "certain petrels of the Humboldt current." Murphy states in regard to these birds: "it is as though such species, so far as their period of reproduction is concerned, had carried their own optimum climate northward with them into the tropics."

In view of the breeding of *S. hirundinacea*, we may assume that a classification into races has not taken place either physiologically nor ecologically. So far such a classification on the basis of habitat characteristics has not yet been made as has already been indicated.

Food Supply: Murphy reports that the food of *S. hirundinacea* consists of "small fishes" of various kinds and "other organisms." He also mentions that the species has been observed to catch "young shrimp" and that it has also been observed to plunge into beds of sea weed, presumably to catch small kinds of arthropods.

Sterna vittata Gmelin (Antarctic sea swallow)

The great similarity between *S. macrura* and *S. vittata* has been known for a long time. In the mating plumage, both species can be easily confused. To judge by the few skins of *S. vittata* which I was able to examine, it would seem that the grey tone of the color is somewhat deeper for *S. vittata* than for *S. macrura*. The white band at the sides of the head under the black cap also appears to be somewhat smaller for *S. vittata*. Murphy reports that the tarsi of *S. vittata* are not as short as for *S. macrura* and that the outer vane on the outer rectrices of *S. vittata* has a lighter gray color. The form of the rectrices also seems to be somewhat different in the two species. Oliver writes that the gray band on the inner vane of the outer wing-end feathers is somewhat broader for *S. vittata* than in *S. macrura*. Concerning the last-named characteristic, *S. vittata* therefore seems closer to *S. hirundo*. There appears to be no statistical study on the range of variation of the species characteristics discussed so that their actual value cannot be estimated.

Distribution: The data in literature on the breeding areas of *S. vittata* are partially erroneous, according to Murphy. According to this author (and in part also according to Peters 1934), there may be 5 races of *S. vittata* which have different areas of distribution along the

coasts of the Antarctic continent and on islands in areas with antarctic and sub-antarctic surface water.

However, Murphy regards the classification into races as unsatisfactory. The species does not seem to breed very far North beyond the limit of the sub-antarctic surface water (cf. Murphy, p. 66). The author named does not list the species for the South American continent and the Falkland Islands. In the following, we briefly review the different races and their occurrence.

1) The sea swallow of the West Antarctic has not received a scientific name from Murphy because its taxonomic position has not yet been cleared up. It is differentiated from the race below primarily by its greater size. The race probably occurs in the West Antarctic, in the South of the Orkney and Shetland Islands. After we have obtained better knowledge through the Gaussberg on the race of "*S. macrura antistropha*" so designated by Reichenow, the latter may show, according to Murphy, its identity with the sea swallow of the West Antarctic. That the sea swallow of Reichenow cannot be related to the species *S. macrura* seems to be perfectly clear. Murphy stresses that genuine Antarctic forms are generally uniform and have circumpolar distribution whereas plants and animals in sub-antarctic regions often show variations of race. He suspects probably justifiably that the race of *S. vittata* residing along the coast of the antarctic continent and the adjacent islands should be called *S. vittata antistropha*.

2) *S. v. georgiae* Reichenow: According to Murphy, this race is probably endemic in South America. It has not been determined whether the race also occurs on the southern Orkney Islands.

3) *S. v. vittata* Gmelin: The race breeds on the Kerguelen Islands, Saint Paul and New Amsterdam but, according to Murphy, not on St. Helena and Ascension Islands as has been stated.

4) The sea swallow of Tristan da Cunha: Murphy also has no scientific name for this race but does not believe it to be identical with *S. v. vittata* as does Peters (1934). According to Murphy, the race breeds on the island group of Tristan da Cunha and Gough Island.

5) *S. v. bollonsi* Mathews and Iredale (= *S. v. bethunei* Buller): The race breeds on the Bounty Islands and has been observed, according to Murphy and Oliver, also on the Snare, Antipode, Auckland, Campbell and Macquarie Islands.

Murphy stresses the fact that the West Antarctic sea swallow is larger than *S. v. georgiae* and suggests that this involves an example of Bergmann's law. The eggs of the larger race are, however, the same size as those of *S. v. georgiae*.

S. vittata is probably closely related to *S. virgata* Cab. which, according to Alexander (1928), breeds on Maria Island, the Crozet Islands, the Kerguelen and Herd Island. Another species with close connections to *S. vittata* is *S. albistriata* (Gray) which breeds along the rivers on the South Island of New Zealand.

Alexander says of *S. vittata* that it is very similar to *S. macrura* and *S. virgata* and that the three species are "in life probably indistinguishable."

Apparently very little is known on the migrations of *S. vittata*. It has been stated that the sea swallow of Tristan da Cunha does not remain in the breeding area during the entire year. On Peter-I Island ("Petermann") in the Western Antarctic, the species was observed to arrive at the breeding places in September and October and to leave them in May. On the Southern Orkney Islands, *S. vittata* arrives in October and leaves towards the end of April. However, it appears to winter on South Georgia. It is apparently not definitely known where *S. vittata* winters but it is possible that the species only wanders about in sub-Antarctic regions during the southern winter.

Food Supply: According to Murphy, *S. vittata* catches "small fishes" and "many sorts of crustaceans." The most important food of the whalebone whales in the South Sea, *Euphausia superba*, according to the joint indications of two authors (Valette and Gain), forms a large part of the food supply of the species in the Southern Orkney and the Southern Shetland Islands. It has been observed that *S. v. georgiae* feeds on *Euphausia* ceans and isopods as well as on "tiny fish." Lönneberg (1906) found fry of *Notothenia macrocephala* in their stomachs. This type of fish, when young, stays in the surface water of beds of sea weed. It has also been noted that *S. vittata* can eat seal meat and lard.

Like *S. macrura*, *S. vittata* therefore seems to prefer pelagic crustaceans as its food.

II. Climatic Factors and Distribution

Murphy writes: "behind the range, migration, and breeding season of sea fowl lies the local climatic cycle. It imposes the regime of existence." When investigating the distribution of a bird species, it is necessary, just as in an investigation of the distribution of other animal species, to consider ecological factors of both existence and distribution as well as historical factors as far as the latter are available. The two types of ecological factors obviously are intimately related to each other. Birds of the body size and type of life shown by the species of *Sterna* are less dependent on so-called microclimatological factors as, for example, land arthropods. Since the species of *Sterna* moreover inhabit sea coasts and the shores of inland water, i.e., biotopes which are always subjected to sometimes violent winds, ecological conditions develop

in such manner that the birds frequently do not come into contact with a microclimate properly speaking because winds are to a certain extent destroyers of microclimate (cf. Geiger 1942). It may be asserted that the species of *Sterna* live in the macroclimatic space such as it is expressed in the local climate. For this reason it may be justifiable to investigate the distribution of this species in connection with the presence of certain meteorological factors. The latter may include such factors as temperature, moisture, precipitation and air turbulence.

It is customary to distinguish between so-called abiotic and biotic ecological factors. The former include meteorological factors and the latter, for example, food supply and the relation to individuals of the same or of another species. The environment acts favorably or unfavorably on the organism. As stressed by Eidmann (1941), geographic distribution is consequently primarily conditioned by ecological factors. Our knowledge of the ecological factors is still very superficial and there are certainly environmental conditions unknown to us. Each species (race) has its specific environment. There are possibly lower units than the presently differentiated races which have a certain special character in relation to environment (ecological races, ecotypes).

Abiotic environmental factors always combine in their action and it is precisely this combination to which the animal reacts. One race may perhaps support a certain temperature in general but when this is combined with a certain degree of moisture, this may no longer be possible. In regard to insects, we know in general that temperature is the most important climatic factor. Which of the climatic factors is most important for the birds cannot be easily decided. Homiothermism renders the animals to a relatively high degree independent of temperature changes. Experiments made in Alberta (Canada) with the migrating *Junco hyemalis* indicate that low winter temperatures may be supported also by a species of birds which normally migrates during the cold season, provided that it has an adequate food supply and is protected from weather. A climatic factor of equally great importance is relative humidity. Apparently we know as yet nothing of its importance for birds. It may be suspected that such birds as the species of *Sterna* which stay over or in the immediate vicinity of water -- as a rule, the young also are in contact from the first moment with relatively moist air -- are dependent on a high relative humidity of the air.

When we are concerned with analyzing the distribution of the species of *Sterna* treated by me in consideration of climatic environment, we must obviously also consider the climatic factors in the wintering areas and, when this is possible, also in the areas of migratory transit. The single factor relatively well known in the greater part of the world is temperature. In the following, I have utilized, as scale of temperature conditions, the average temperatures of certain months. These mean temperatures as a rule do not indicate a great deal on the ecological position of the species of birds. In order to form an opinion on the

importance of the temperature factor, we must take into account the changes of temperature during the 24-hour day and during different periods. The changes during 24 hours, however, can never be particularly high for these species of *Sterna* because they breed primarily along sea coasts and generally in the vicinity of the water. Undoubtedly, the species of *Sterna* are habituated and probably also adapted to a pronounced maritime character of temperature variations. *S. hirundo* which is also numerous along inland waters, is perhaps more tolerant in this regard than the others. The variations during the 24-hour day at inland breeding places are probably relatively high, especially during the breeding period in the late spring and early summer, by comparison with the conditions along sea coasts.

In view of the occurrence of the species of *Sterna* along sea coasts, I selected as a rule August and February as the warmest months because the temperature of the sea water is highest during these months.

S. hirundo breeds in an area which extends from the North Cape as far as Florida and Southern Iran. In the North, it therefore breeds in the Arctic climate where the warmest month does not exceed $+10^{\circ}\text{C}$ and, in the South, in strictly subtropic climate with high summer temperatures. The species winters in an area stretching from the sub-Antarctic to the equator; in South America, the wintering area is tangential to the $+10^{\circ}\text{C}$ isotherm of the warmest month. *S. hirundo* appears to be eurythermic. However, it is only possible to say in regard to its dependence on temperature that it is restricted during breeding to the temperate zone in the larger sense but appears to be more tolerant in regard to temperature outside of the breeding period because it then also occurs in the tropical zone. Although *S. hirundinacea* is not distributed over as large an area as *S. hirundo*, it appears to be more eurythermic in regard to dependence of temperature than the latter because it breeds from Tierra del Fuego and on the West coast of South America to about 5° Southern latitude. On the east coast of South America, it extends as far as the Tropic of Capricorn where similar temperature conditions prevail during the warmest months as at the Northern limit of the species on the West coast. The distribution of *S. hirundinacea* appears to be more closely connected, however, with nutrition-biological conditions (see below) than that of *S. hirundo* so that we can state so far only that it is relatively eurythermic.

S. vittata and *S. macrura* show a different reaction to temperature factors. The former species occurs mainly in an area where the temperature of the warmest months does not exceed $+10^{\circ}\text{C}$. Only the contingents of Tristan de Cunha and Gough Island inhabit a warmer region where the warmest month is probably not more than about $+15^{\circ}\text{C}$ (cf. Fig. 8). In the area of the Pacific, the town of Wellington on the South coast of New Zealand has an average temperature in January and February of $+16.7$ and/or 16.6°C but *S. vittata* probably does not breed this far North. Outside of the breeding period, the species does not appear to wander in regions with higher temperatures. However, it should be stressed that the

knowledge of the distribution and migration of the species is rather insufficient and that it is rather difficult to distinguish them from *S. macrura* at some distance. However, it seems to be quite apparent that *S. vittata* has another reaction to the temperature factor than the two species of *Sterna* treated earlier. *S. vittata* is quite apparently not as eurythermic. It prefers lower temperatures during the breeding period and does not seem inclined to remain, during the remainder of the year, in regions with higher temperatures. According to our present knowledge, *S. vittata* occurs mainly in a region where the average temperature of the warmest month varies between $+10^{\circ}\text{C}$ to perhaps $+10^{\circ}\text{C}$. It would seem accurate to classify the species animal-geographically as Antarctic-subantarctic.

In view of the distribution of *S. vittata*, I believe it justifiable to accord greater significance to climatic factors than to nutritional biology because the species is apparently able to obtain its food also in extensive areas outside of the present breeding area. The temperature factor would appear primarily to determine the distribution of the species.

The species last mentioned corresponds, in regard to distribution, to *S. macrura* in the Northern Hemisphere. The latter is probably found mainly north of the July isotherm of $+10^{\circ}\text{C}$ and has been observed to breed at points with snow still on the ground. *S. macrura* also breeds in regions of Europe where the temperature of the warmest month is between 15°C and 20°C and occurs in the eastern United States so far South that the same month here at the coast has an average temperature of about $+20^{\circ}\text{C}$. Considering this, the species is more numerous and has larger populations in and in the vicinity of regions of the Northern Hemisphere where the average temperature amounts to $+10^{\circ}\text{C}$. In Siberia, the July temperature in the breeding area of the species does not exceed $+5^{\circ}\text{C}$ over long stretches of the coast. The distribution of *S. macrura* in the Atlantic region is therefore rather surprising in view of the temperature factor. It would appear that this species is more tolerant to temperature than *S. vittata*. On the other hand, it seems to be greatly attracted by regions with temperatures which correspond to those occurring in the larger part of the breeding area of *S. vittata*. Consequently, there may be factors which influence *S. macrura* more strongly than only the temperature factor.

In the area of the Pacific Ocean, the distribution of *S. macrura* also has some peculiar features. Towards the Northeast-Asian side, the species does not extend further south, according to the credible data in literature, than the Chuckchee Sea i.e., there is never an average temperature of more than $+10^{\circ}\text{C}$ in its Asian breeding area during July or August. The species consequently here occurs only in a strictly arctic climatic region. On the Northwest coast of North America, *S. macrura* breeds in a coastal area where the temperatures of July and August are $+15^{\circ}\text{C}$ and less. The distribution of the species towards South here extends

much further than on the Northeast-Asian coast. The distribution of the species in the northern reaches of the Pacific Ocean therefore also shows peculiar characteristics.

In the hibernating areas of the Southern Hemisphere, the average temperature of the warmest month does not exceed $+20^{\circ}\text{C}$ and the species has been observed towards the South in exclusively Antarctic and sub-antarctic regions. At present, it is not possible to decide where the most important wintering areas of the species are located but it appears to react to the temperature factor during the hibernating period in the same manner as during the breeding period and is therefore differentiated from *S. hirundo* by the fact that it has no higher tolerance to temperature during wintering. The attempts undertaken here to interpret the distribution of the four species of *Sterna* in relation to the temperature factor do not afford any very reliable basis for its understanding. Strictly speaking, we can only assume as quite probably that the different species have a somewhat different reaction to the temperature factor and that *S. vittata* is doubtlessly the one adapted to the lowest temperatures which may be around -5 and -10°C during the breeding period. Approximately the same reaction appears to be applicable to *S. macrura*. However, both species also breed in areas with an average temperature of about $+15^{\circ}\text{C}$ of the warmest month and so show a relatively high degree of tolerance to temperature or eurythermism. The tolerance to temperature of both species is even more effective than that of *S. hirundo* and *S. hirundinacea* which breed in areas where the average temperature of the warmest months lie between $+10$ and about 25°C . *S. macrura* and *S. vittata* are more closely bound to the subarctic and arctic and/or subantarctic and antarctic regions whereas the two other species occur in numbers in extensive temperate areas and where *S. hirundo* is apparently most definitely restricted to such areas. It would seem as if the two species which are most closely bound to the lowest temperatures, have a somewhat higher degree of eurythermism than the species which breed in temperate areas.

Stresemann cautions against attributing too much significance to climatic factors in the interpretation of the distribution of the species of birds. Birds possess a very effective body-heat control. Because of the absence of sweat glands and the presence of their feather coat, they are well protected against heat loss. It is therefore easily understandable that birds can support very low temperatures, provided that they have suitable food and that they are able to procure and ingest the quantity of food necessary for generating body heat. It is therefore also very probable that birds are quite independent of the air temperature and to a higher degree than mammals. Many species of birds are therefore by their manner of life also exposed to irregular and probably not infrequently very great and rapid temperature changes. We need only think of the large temperature variations which exist on a sunny day between the very shallow layer of air close to the heat-absorbing surface of the ground and the air at a height of a hundred meters to which certain species living close to the ground not infrequently ascend. We should moreover

also consider the high temperature variations between day and night to which species living close to the ground are exposed in early summer and late spring. Such temperature extremes cannot be avoided by the birds through digging-in. However, for adult birds, we might consider the possibility that they are able to escape from a too highly unsuitable abiotic environment by means of their wings. However, this is not possible for the young of species living close to the ground. Especially eggs and the nest young are in this regard subject to the greatest danger if they are not protected by the parents. On the northernmost and southernmost breeding places of *S. macrura* and/or *S. vittata* as well as in other locations, eggs and young may remain perhaps frequently uncovered while the parents are searching for food. They are then in direct contact with the cold air. The best protection for eggs and young against cooling off or freezing may consist in the fact that they are able to absorb the not insignificant heat of the sun in even high geographic latitudes because of their relatively dark colors. The dark color of the eggs and on the back of the young is therefore in my opinion a protection against heat loss during the absence of the parent birds. The ground in the vicinity of the nest obviously also has a heat-absorbing capability. The occurrence of the species of *Sterna* near the Poles can therefore be explained from the viewpoint of body-heat regime.

We may raise the question of the manner in which the birds register temperature. The thick feather coat as well as the horny protection of the lower extremities and the bill constitute insulation. However, there is an organic system which is in contact with the air over its entire large surface, i.e., the trachea, the capillaries of the lungs and the air sacs. Of course, air does not reach these organs without preheating but the latter is based on the respiratory frequency and the latter is related to the activity of the bird. The air probably reaches at least the upper respiratory ducts (nostrils, nasal cavity, throat and trachea) relatively cold. During flight, when the respiratory movements of the body are probably hindered and the air enters mostly passively, the respiratory ducts probably also come into contact with not very much preheated air. It does not seem excluded to me that, precisely in the upper respiratory tracts mentioned, there is located an organ for temperature registration. One form of temperature awareness does seem to exist in birds as indicated by certain observations on the behavior of migratory birds. Living tissues with nerves and blood vessels lying close to the surface, which come with the exterior air into direct contact, are possessed by birds precisely only in the respiratory ducts.

On the assumption that the temperature of the air is of some importance for the wellbeing (and consequently also for the distribution and occurrence) of the birds, we shall discuss briefly other climatic factors which are probably of importance for the distribution of the birds and their selection of localities. It would seem even more difficult to determine the significance of relative humidity than that of the temperature factor. On its way to the lungs and the air sacs, the respiratory

air becomes strongly moist very soon. Especially the nostrils and the nasal cavity will come into contact with the moisture existing in the air and it may well be imagined that the birds have the capability in the mucosae of these parts of the respiratory system to register changes of air moisture. However, it is also possible that they may perceive variations of moisture indirectly in response to the action on the latter of their feathers. The significance of relative humidity for distribution and occurrence of the birds has been considered very little. The species of *Sterna* must be accustomed to high relative air moisture. However, newly hatched or in the initial downy stage, they are probably subject to great changes in relative humidity because the latter may drop strongly (by 40-50% according to my own observations) under certain circumstances along sea coasts close above the surface of the ground (sand, pebbles, rubble or smooth rock).

It is apparently difficult to determine in detail the significance of the amount and distribution of precipitation, cloud cover, fog and wind for the distribution of the birds. However, these factors probably definitely have an influence. High winds are avoided by many birds and nesting places are preferably located in the lee of the wind. Rain accompanied by high winds is probably a combination of factors which reduces the activity of several species of birds. The species of *Sterna* in their character as aquatic birds and to a high degree as coastal birds are probably less hindered in their distribution by strong precipitation or strong wind. This is attested by their present distribution. A correlation between the distribution of the species here treated and the distribution of precipitation, cloud cover or prevailing winds has not been discovered (cf. Schott 1926, 1935, maps). Fog as ecological factor should probably not be entirely neglected. Schott (1935) writes: "high frequency of fog is an adverse phenomenon and a nuisance for someone seeking the healing forces of the sea also because of the exclusion of sunshine occurring simultaneously." The waters around Kamtchatka and the Kurile Islands as well as the Sea of Okhotsk have a great deal of fog. Schott mentions that 40% of the days are foggy during the months of June, July and August. Around the Northern Kurile Islands and the Southern tip of Kamtchatka, days of fog are even more than 50%. He mentions specifically for the Sea of Okhotsk that days of fog are numerous and the fog very dense. In the Atlantic Ocean beyond Newfoundland, there is an area with 40% of days of fog during June, July and August (Schott 1926). Fog interferes perhaps in part with the production of phytoplankton by excluding solar radiation and this also hinders the production of zooplankton of different kinds. In regard to the lack of sun on Iceland and its influence on life, Timmermann (1938) writes: "very disadvantageous for proper growth and development of a higher fauna and flora is also the pronounced lack of sun of the country which, however, seems to be cancelled out in its biological effect in part by more intensive ultraviolet radiation."

S. macrura probably has poor nutrition-ecological living conditions in very foggy areas. It is possible that fog also interferes with the search for food of the species. The absence of the species from the very foggy Sea of Okhotsk is probably in part due to the conditions mentioned above. However, *S. longipennis* does occur along the shores of this sea which is possibly explained by the fact that this species nourishes itself to a higher extent than *S. macrura* from other organisms than those falling under the designation "pelagic." There are apparently no indications in literature on how numerous *S. longipennis* is in these regions. We should also not entirely neglect the fact that the reduction of solar radiation due to fog must also have a negative influence on the growth of the young. Especially *S. macrura* with its principal distribution in subarctic and purely arctic regions is probably adapted to long days with much light and its young grow during the period of greatest light.

An examination of the connection between the distribution of the species of *Sterna* and certain climatic factors has had as only result, in view of our insufficient knowledge of the demands of the species on the abiotic environment, that the temperature factor probably plays a certain role. *S. macrura* and *S. vittata* seem to exhibit other characteristics of adaptability to the latter than *S. hirundo* and *S. hirundinacea*. It will probably involve considerable difficulties to investigate the reaction of species of *Sterna* to the temperature factor experimentally. It is possible that fog indirectly influences the distribution of *S. macrura* by strongly reducing the penetration of solar radiation into the top layer of sea water and consequently also the production of living organisms by the sea which are suitable as feed for *S. macrura*. Too high a drop of the number of hours of sunshine may possibly also disadvantageously affect the propagation of the species.

We should also keep in mind that the climate affects the ability to compete of the animal species. This viewpoint may be applicable to *S. macrura* and *S. hirundo* and therefore contribute to an answer for the question of the causes of the different distribution of the two species. Since *S. macrura* has a shorter breeding period than *S. hirundo* (21-22 and/or 21-30 days) and also requires a shorter time for developing the young to the flying stage (about 3-4 weeks), the species first named must be more suitable for the arctic summer than the latter. An advantage from the shorter ontogenesis in temperate areas is not very probable. We may also suspect that the quicker growth of the young of *S. macrura* is not as suitable for regions with warmer water and shorter days because the supply of food is here less as well as that part of the 24-hour day which can be utilized for the search for food.

Other biological factors may also be included. *S. hirundo* derives greater competitive force because it has a larger hatch (usually 3 as against 2) of eggs compared to *S. macrura*. Both species possibly also have somewhat different demands as to the nesting ground (Dirksen 1932) which may also have an influence on the distribution of the populations.

Pasture land seems to be preferred by *S. hirundo* whereas *S. macrura* preferably lays its eggs on ground with little or no vegetation and consisting of smooth rock, pebble, rubble, sand, etc., according to several authors (cf. Durango 1945).

III. The Propagation of the Four Species of *Sterna* Within the Breeding and Wintering Areas Together With Hydro- logical and Nutritional Factors

S. hirundo appears to be the least demanding of the four species in regard to environmental factors and shows, in its distribution, no special or noticeable relations to water temperature, salinity, color of the water, or sea currents. Temperature and salinity of the surface water are very important for the production of microorganisms. That of phytoplankton is somewhat reflected in the color of the surface water. Pettersson (1939) describes the situation as follows: "the color of the sea constitutes to a certain extent a measure for the content of particles of the water,..." (in Swedish original). The particles are both organic and inorganic. The color of sea water is measured with the so-called Forel color scale. In the central areas of subtropic and tropic ocean regions on both sides of the Tropics, the color of the sea water is blue and it is said that blue is the desert color of the sea. Optically pure sea water is blue and its content of plankton in the ocean areas named above is low. Sea water along the coasts is green or green-yellow and surface water in areas with cold sea currents and ascending cold currents has the same color. In the higher geographic latitudes, sea water therefore is uniformly green-yellow or green or sometimes also greenish-black colors and sometimes yellowish-brown (cf. Fig. 12). However, blue water also occurs in the Polar regions. The shading of the color into green or green-yellow is due under present assumptions, according to Pettersson and Steemann-Nielsen (1944), primarily to the influence of a yellow pigment which is considered as closely related to humus substances. It is believed that the yellow pigment consists of decomposition products of phytoplankton. The deeper the greenish or green-yellow color of sea water, the greater its content of phytoplankton.

Cold sea water contains more gases and more dissolved nitrogenous components as well as dissolved phosphates than warm sea water and the former are important for the development of phytoplankton (Fig. 13). Cold water has a lower salinity than warm sea water. According to Murphy, phytoplankton is "far more abundant" in cold sea water than in warm because of the differences in the composition of the water. Cold shallow coastal waters with low salinity are rich in phytoplankton (Fig. 10, 11, 12, 14, 15, 16). At least in part due to the greater angle of the sun in higher geographic latitudes, the layer of water producing plankton generally is restricted to a depth of 100 m. Such phytoplankton constitutes the food supply of fish fry and different small types of fishes as well as of pelagic crustaceans and molluscs (Fig. 16). Phytoplankton might be designated as the basic foodstuff and all animal life

in the sea from the smallest crustaceans to whales (Fig. 10, 12) and various sea birds (Fig. 16, 17, 18) is directly or indirectly dependent on it.

There is another primary reason why cold waters are richer both in phyto- and zooplankton than warm waters. The investigations of Loeb (1908) have shown that the span of life in cold water is greater than in warm, i.e., many more successive generations of the same species are able to exist simultaneously at 0°C than at $+10^{\circ}$ or $+20^{\circ}\text{C}$ (Murphy, p. 64). For example, if the temperature drops by 10°C , the span of life is increased about 1,000 times but the corresponding development periods should be multiplied only with a factor of about three.

Because of its dependence on the hydrological factors discussed above, the natural home of abundant plankton production therefore lies in cold water, i.e., arctic and subarctic and/or antarctic and subantarctic waters. However, there water is displaced at certain locations by sea currents rather far into lower geographic latitudes and there are strong contrasts between subarctic and/or subantarctic water and subtropical water in certain coastal regions (Fig. 10, 11). I have here divided the antarctic and subantarctic waters on the basis of the same principles as Murphy (p. 68 and 72) and therefore limited the collective antarctic and subantarctic zone northward from the subtropical zone by the surface water isotherm of the coldest month of $+11.5^{\circ}\text{C}$ and that of the warmest month of $+14.5^{\circ}\text{C}$. In view of the breeding and hibernation habits of sterna, interest is completely concentrated on the summer temperatures. For the sake of simplicity, the average temperature of the surface water of the warmest month has been rounded off to $+15^{\circ}\text{C}$. The areas of arctic and subarctic surface water, I have limited in the same manner. Salinity in the subantarctic and/or subarctic areas rises to 3.45% (3.5%).

Helland-Hansen and Nansen (1909) designate as arctic that water which has a temperature of $0-2^{\circ}\text{C}$ and a salinity of 3.46-3.49%. Polar water never has temperatures above 0°C and is "practically a desert," according to Nansen (1925). Consequently there are two ocean deserts, i.e., the region of surface water of the tropics and that of polar waters. The combination of Polar and Atlantic waters produces, according to Hjort and Ruud (1929, p. 89), layers of water with temperatures of $0-6^{\circ}\text{C}$ in which arctic water is characterized by temperatures of $0-2^{\circ}\text{C}$ and "boreal" water by temperatures of $3-6^{\circ}\text{C}$. Boreal water in this definition corresponds to subarctic water. In agreement with Murphy's definition of subantarctic water, however, I permit subarctic water to have maximum summer temperatures of 14.5°C (15°C).

Pelagic crustaceans typical for the Southern Hemisphere consist of Euphausiaceans and the most important species of the antarctic regions is probably *Euphausia superba* which constitutes the main food of penguins and other sea birds as well as of whalebone whales at certain times. Another species in regions of antarctic water is *E. frigida*. *E. vallentini* and *E. longirostris* are encountered in subantarctic regions. However, in

the latter regions Euphausiaceans do not have the same dominant role as bird and whale feed. Very important are the anomura of the family Munida, with special emphasis on *M. gregaria* which is a pelagic crustacean, typical for subantarctic surface-water areas, in the Grimothea stage. *M. gregaria* is very important both as food for birds and for whales. Plankton production is greatest during the summer, i.e., during the breeding period of the sea birds and during the wintering period of the species of the Northern Hemisphere in the Southern Hemisphere.

It is not possible to speak of a harmonious distribution of surface-water zones any more than in regard to that of the air. This has several reasons. We have already mentioned above the ocean currents which displace cold water far into regions of warm surface water of the lower geographic latitudes. The Labrador current extends as far as Cape Hatteras, even though it has lost in intensity; the current from the Canaries ("Kanarenstrom") flows southward along the west coast of North Africa as far as 20° latitude; and the current from the Falklands ("Falklandstrom") can at least temporarily influence the water as far as Rio de Janeiro and does so permanently as far as the geographic latitude of the Rio de la Plata. The cool "Benguela" current reaches as far as Loanda. In the Pacific Ocean, cold currents flow from the Bering Sea and the Sea of Okhotsk as far as Hokkaido (Oya-Schio). A more intense cold water current flows along the west coast of the United States from the North as far as the Tropic of Cancer and there is also the Humboldt Current which carries water from the subantarctic surface-water zone as far as the coast of Peru and South of the Equator. There are also warm currents which penetrate far into cold water regions. Another circumstance also disturbs the division into zones which is the existence of ascending cold currents ("cool belts of upwelling"). Coastal regions with such water are located on the west side of the continents (cf. Fig. 10, 11) but also occur along the east coast of northern Argentina. Such ascending depth currents produce high temperature anomalies of surface water in tropic and subtropic regions and are characterized by similar hydrological conditions as the surface water of higher geographic latitudes and have the same abundance of plankton.

Obviously, the surface water of a (cold) current entering regions with warm water increases in temperature, but does retain many of its characteristics from the higher latitudes. The biological content, for example, still possesses characteristics of the region of origin of the surface water. We can cite as an example for this that, in the water of the Humboldt Current beyond the Peruvian coast where the temperature of the surface water reaches 20°C and even more during the summer, the Grimothea-stage of *Munida* occurs abundantly at times (Murphy, p. 73). *Munida* is a typical subantarctic crustacean and is not found at Tristan da Cunha in the Middle South Atlantic near the subtropical convergence.

As already mentioned, *S. hirundo* appears to have no particularly observable relation to the hydrological factors mentioned in regard to distribution. *S. hirundinacea*, the coastal sea swallow of the South American continent, very definitely does show such a relation. It occurs on the east coast as far northward as the Falkland Current still has an influence, i.e., in other words as far as the region of the warm "Brazilian" current. On the west coast, the species is found as far northward (toward the equator) as the Humboldt Current and as ascending depth currents transform hydrological conditions. *S. hirundinacea* is regarded by Murphy as a very typical subantarctic species but occurs in extensive areas where neither the temperature of the air nor that of the surface water are typical of the subantarctic region (Fig. 6). The species of *Sterna* are probably relatively independent of the temperature of the water even though they may probably be aware of it. The temperature of the water is probably of no great significance for species of birds which come into contact with it only during the brief moments of catching their food. For this reason, salinity also probably has no great significance. We are therefore justified in suspecting that the occurrence of certain food animals exercises a decisive influence on the distribution of *S. hirundinacea*. It occurs in the coastal waters of South America which are rich in plankton. When considering the breeding habits of the species (cf. p. 23 of original), climatic factors with emphasis on temperature probably also play a certain role in its distribution. *S. vittata* inhabits exclusively the cold surface water zone of the Southern Hemisphere. It has already been indicated earlier that temperature is probably of importance for the occurrence of the species. Observations on the selection of the food of the species indicate that specialized food plays a very great role (euphausiaceans). However, we are justified in suspecting that food does not play a completely dominating role because the species would otherwise occur in the areas of the Falkland and Humboldt Currents. According to our knowledge, it is completely absent from the coast of the South American continent. It is possible that the species possesses no intensive drive toward distribution because of its low rate of propagation with only one or two eggs and also because it is not especially resistant to wind. *S. vittata* has possibly not been able to settle along the coast of the South American continent because it has been unable to compete with the appreciably larger and probably stronger *S. hirundinacea* which is extremely numerous here and apparently has basically the same nutrition and breeding factors as *S. vittata*.

In summation, we might possibly list four factors of importance for the distribution of *S. vittata*: temperature (the air), specialized food supply, competition with *S. hirundinacea*, and winds (since the species seems less resistant to strong winds).

S. macrura breeds on the Northern Hemisphere equally as far toward the North Pole as *S. vittata* toward the South Pole on the Southern Hemisphere. It is distinguished from *S. vittata* by the fact that it extends

far into the temperate zone along the coasts of the Atlantic in Europe and North America. We have already expressed the opinion that the species, in spite of its rather high tolerance to temperature, is still pretty much dependent on the low temperatures of the Arctic and Subarctic areas. In regard to salinity, the species is probably not very sensitive because it occurs in sweet water as well as in brackish and salt water areas but the salinity of its breeding area should not be any higher on the average than 3.5%.

In the region of the North Sea and the Baltic Sea, *S. macrura* is found along water which exceeds an average temperature of 15°C during the warmest months but does not rise above 20°C and is about +15°C during the actual breeding period. Although the species extends further south along the East coast of North America than in Europe, it is never found along water with a temperature of more than +15°C in August but the temperature of the air is here slightly higher than in the southernmost part of the European breeding area (Fig. 3, 8, 10).

The reason for the southward extension of *S. macrura* along the east coast of North America lies with considerable probability in the Labrador Current which prevails as far as Cape Hatteras. The fauna of these waters have much in common with that of the arctic and antarctic waters. Plankton is abundant as reflected in the fact that there are rich fishing banks beyond the coast of Newfoundland and Nova Scotia. In the Gulf of the St. Lawrence and in the northern parts of the Newfoundland banks, *Phoca groenlandica* and *Cystophora cristata* have important breeding areas, according to Nansen (1924). The young mainly feed on small crustaceans and pteropods (*Clione limacina*). The existence of especially suitable food for the young is the real reason for the long migration of the seals toward certain breeding areas. According to Wynne-Edwards (1935), *S. macrura* is numerous in the Gulf of St. Lawrence and Lincoln (1935) reports them as breeding on the north shore of the Gulf. Ingebrigtsen (1929) mentions that *Balaenoptera musculus* is caught in considerable numbers off the coast of Newfoundland. Nutritional factors consequently favor the aggregation of seals and whales as well as *S. macrura* in the waters just mentioned.

Lincoln (1935) states that *S. macrura* definitely is most numerous along the west coast of Greenland, the Davis Straits and Baffin Bay. Hydrological conditions here during the summer favor the production of abundant plankton with a large share of euphausiaceans (Hjort and Ruud 1929). Especially outside of Disko Bay and south of the latter, euphausiaceans occur in abundance. Whales are also caught here in numbers (*Balaenoptera borealis*, *B. physalus*, *B. musculus* and *Megaptera nodosa*). Breeding places of *S. macrura* are found especially in the fjords south of Disko Bay (North and South Ström fjord, etc.). The western part of Baffin Bay and Davis Straits is traversed by a cold polar current which reduces plankton production and consequently the existence of whales and apparently also of *S. macrura*.

Hjort and Ruud (1939) show the high concordance of phenology along the west and north coasts of Norway for *Meganyctiphanes norvegica* and *Thysanoessa inermis* with that of *Megaptera nodosa* and *Balaenoptera physalus*. In Finnmarken, there are whaling stations for hunting *Balaenoptera physalus* and *B. musculus*. At the edge of these northern waters are found the largest Scandinavian colonies of *S. macrura*. The species begins to breed along the Norwegian west coast beginning approximately at 60° northern latitude. Especially along these coastal areas, *Meganyctiphanes norvegicus* occurs in numbers from the middle of May until the middle of August (Hjort and Ruud 1929), i.e., the time when *S. macrura* stays here. In the North Sea and in the Baltic Sea, the species lives along water, the temperature of which can no longer be included in the Subarctic surface water region. The explanation for the relatively large number of the species in these areas is probably a question of food supply. The waters of the North Sea and the Baltic Sea contain much plankton probably because they are shallow; fishing here yields an ample catch. The distribution of *S. macrura* in Scotland also shows that the species depends on an abundance of plankton and is most numerous in Western Scotland. The greatest number of whales is caught along the coastal banks of the west coast so that we may assume a casual connection between the occurrence of whalebone whales and *S. macrura* on the one hand and an abundance of plankton on the other hand. The investigations of Jespersen (1925) clearly show the dependence of sea birds on the regions of the Northern Atlantic rich in plankton (Fig. 18). The coastal waters of Nova Scotia and the waters between Iceland and the British Isles are abundantly populated by birds. He lists fish fry, copepods, amphipods, "lightning crabs," cuttlefish and worms as important macro-plankton and mentions that some birds, e.g., *Rissa tridactyla*, live directly on the small crustaceans listed. The birds are therefore indirectly dependent on plankton which is the food of the small fishes on which they feed. Jespersen stresses that the waters around the West Indian Islands and the Saragossa Sea are poor in plankton and birds. Certain species of birds (e.g., pelicans, tropic birds, Frigate birds) are encountered here but never in the same numbers as those species in the northern part of the Atlantic Ocean living on plankton.

In the northern Pacific Ocean, the distribution of *S. macrura* shows the already mentioned peculiarity that the bird breeds in northeast Asia on the Chuckchee Peninsula. The absence of the species in cold water further South was related by me to the fogs of the region which probably cause a lessened production of plankton, lessened possibilities of food procurement as well as poor environmental conditions for the development of the young. *Balaenoptera musculus* which demands food similar to *S. macrura* migrates along the northwest coast of North America as far as the Bering Sea but along the east coast of Asia not as far as the same latitudes and is not usually encountered in the waters around Kamtchatka (Ingebrigtsen 1929). The northeast Asiatic waters therefore appear to be unsuitable also for this species of whale. The probably most important reason in any event for the absence of *S. macrura* in any larger area of northeast Asia must probably be sought, however, in hydrology. The current

passing south through the Bering Straits is very insignificant and warm water does not penetrate north through the island chain of the Aleutians. The mixture of water suitable for an abundant plankton production therefore takes place in the western part of the Bering Sea not to the same degree as in the northwestern Atlantic Ocean. The coastal waters of the western part of the Bering Sea probably contain an insufficient amount of food for *S. macrura*. The hydrological conditions constitute to some extent an analogy to those of the western areas of Baffin Bay and Davis Straits where *S. macrura* appears to be more infrequent than in the eastern areas. That the species occurs no further southward in the Japanese high-sea fishing banks is probably connected with the fact that the required climatic factors are no longer operative (temperate monsoon climate) and the surface water is presumably generally too warm which may bring it about that certain pelagic animal forms suitable for the species no longer occur on the surface. On the northwest coast of North America, *S. macrura* occurs southward as far as the sub-tropical convergence, i.e., it lives entirely in arctic and sub-arctic surface water areas. Here there is also a region of large fishing beds with high yield. According to Ingebrightsen (1929), "Krill" (euphausiaceans) are found amply along the west coast of North America and in the banks of the Bering Sea. However, it is difficult to understand why the species does not occur further southward because the temperature of the surface water as far as Central California is rather low which is in part due to the influence of ascending cold depth currents (cf. Fig. 11). Along the coast of the Northern Antarctic, *S. macrura* breeds customarily, according to Stegmann, and the coastal waters abound in plankton.

The regions sought out by *S. macrura* for wintering correspond to the breeding areas in regard to climate. We see from Figs. 10, 11, 12 that they are also characterized by sea water with similar hydrological factors. Its wintering area on the coast of Southwest Africa has surface water which maintains itself at a temperature of about $+15^{\circ}\text{C}$ even during the warmest month (southern summer). The average temperature of February and November in the coastal range is $+20^{\circ}\text{C}$. Along the coast of South America, *S. macrura* can be found to our knowledge during the southern summer primarily there where the water has sub-antarctic character. The surface water in this wintering area of the species probably does not exceed an average temperature of $+15^{\circ}\text{C}$ during the months of November and February. The immense abundance of pelagic crustaceans existing in these waters during the southern summer probably influences the species to a high degree in the selection of wintering areas. During the southern summer, *S. macrura* has also been observed outside of the Ross Sea. As shown in Fig. 11, there are important whale-hunting grounds precisely in these last named waters which is definite proof of the wealth of the surface water in plankton and pelagic organisms. Ingebrightsen (1929) reports that *Balaenoptera musculus* has been encountered during the southern summer in "enormous numbers" in the waters between the southern Shetland and Orkney and also the Sandwich Islands as well as in the Weddell and in the Ross Sea.

Research seems to indicate that *S. macrura* and *S. vittata* have a predilection for certain food (standard food range) which coincides to a high degree with that of the whalebone whales. Fish fry, pelagic crustaceans (euphausiaceans) and mollusks (pteropods) have been found in masses in the stomach of whales, according to literature. The herring whale (*Balinoptera physalus*) living along the southwest coast of Norway, according to the observations of Hjort and Ruud (1929), feeds on herrings (*Clupea*), *Calanus*, *Thyssanoessa inermis* and *Meganyctiphanes norvegica*. The last named animal species is the main food from May to September. Other whalebone whales have a similar standard food range. It is of interest to note here that the whalebone whales are found mainly in the same areas in which *S. vittata* and *S. macrura* also occur. Fig. 10 and 12 show the southern limit of distribution of the whalebone whales for the Northern Atlantic Ocean and the northern limit for the Southern Atlantic Ocean. The border lines coincide quite well with the limits between surface water with a salinity of 3.5% and waters of higher salinity. In the Northern Atlantic Ocean and along the coasts of Southwest Africa and Southeastern South America, this delimitation coincides with the outer limits of the regions with prevaillingly green surface water (9% yellow according to the Forel scale). Whalebone whales also occur mainly in surface water whose temperature may be classed among that of the polar and sub-polar regions. They consequently occur in waters with an abundant food supply (cf. Jespersen 1925). It is of interest to note that the whalebone whales occur outside of these regions along the southwest coast of Africa as far as the Benguela Current and ascending depth currents have an influence, i.e., as far as the latitude of Gabun. They follow the Falkland current as far as the latitude of the Rio de la Plata. There are strongly utilized wintering localities of *S. macrura* along the coasts of Africa and South America mentioned above (Fig. 3). The breeding and wintering areas of *S. macrura* in the Atlantic Ocean further coincide in the areas of distribution of the bi-polar species of *Mystacoceti* *Balaena glacialis*, *Megaptera nodosa*, *Balaenoptera musculus*, *B. physalus* and *B. borealis*. On the Southern Hemisphere, the wintering areas of *S. macrura* and the area of distribution of the species of *Mystacoceti* coincide surprisingly well (cf. Schott 1926, p. 285 and Ingebrigtsen 1929), except with this difference that the whales on the West coast of Africa extend further northward than *S. macrura* during wintering. Ingebrigtsen reports that *Balaenoptera musculus* stays during the southern summer along the west coast of Africa as far as 10° southern latitude but the food supply for the whales is apparently already poor north of 30° southern latitude because the whales within these waters are no longer so well-fed that it is profitable to catch them. On the Northern Hemisphere, the whalebone whales mentioned are found within the larger and southern part of the Atlantic breeding area of *S. macrura*.

Whalebone whales have been encountered also outside of the areas of distribution mentioned above. There have been findings of *Megaptera nodosa* on the American East coast around Cape Hatteras where sub-arctic

water still does exercise an influence but the species has been observed occasionally also in the Caribbean Sea. On the American East coast, the species has then again been observed only directly south of Cape San Roque and in the region of Bahia. These finds are probably connected with migration because the species travels in spring to warmer waters for breeding. The animals may then become scattered in the Northern Atlantic Ocean rather far South and in the southern part of this Ocean rather far North. Along the eastern coastal belts of the Atlantic Ocean i.e., on the West coast of Europe and Africa, whalebone whales have been found frequently outside of their usual areas of distribution. *B. borealis*, *M. nodosa* and *B. glacialis* have been encountered in the area outside of the Pyrenean Peninsula and Northwest Africa as far as the Tropic of Cancer. Between Cape Blanco and Gabun, Schott does not mention any finds of whalebone whales but they do occur, beginning with the town last named, on the equator along the southwest coast of Africa as far as the waters outside of Cape Town. The finds of whalebone whales outside of the customary areas of distribution are therefore more frequent in the eastern coastal waters of the Atlantic Ocean than in the western. Actually, the African coastal waters from the equator southwards are generally included in the area of distribution of *M. nodosa* and *B. musculus* and perhaps also of *B. glacialis*, according to Schott. In the western coastal waters of the Atlantic Ocean, whales are encountered only infrequently in the area between Cape Hatteras and Bahia Blanca (Argentina). The finds of certain whalebone whales in the eastern coastal waters of the Atlantic Ocean and in the area of distribution of *B. musculus* and *M. nodosa* are located on the migratory paths of *S. macrura* along the west coast of Europe and Africa. It is also of interest to note that a presumably less utilized migratory path of the species leads from Cape Verde to the east coast of South America in the region of Cape San Roque and further southward from there, i.e., precisely over the waters where some finds of *M. nodosa* have been made (Fig 3, 17).

In the arctic region of the Atlantic Ocean and in Hudson Bay, *S. macrura* occurs in regions inhabited by the purely arctic *B. mysticetus* which feeds primarily on pelagic crustaceans and pteropods, i.e., the same food as consumed by *S. macrura* in arctic regions.

A comparison was therefore made between the distribution of the species of *Mystacoceti* mentioned above and of *S. macrura* and *S. vittata* because the whales and these species of *Sterna* occur in areas with the same cold surface water rich in plankton. It has been demonstrated that they make highly similar demands on their types of food. In my opinion, it is primarily the ecology of nutrition which conditions to a large extent the distribution of the two animal species, although the ecological factors otherwise act quite differently on whalebone whales and these species of *Sterna*. Stresemann stresses that the surface water isotherm of +21°C in June coincides with the southern limit of the breeding area of *S. hirundo* in the Atlantic Ocean and points out that the water temperature has no direct significance for the distribution of the species but influences it indirectly by the circumstance that preferred food animals

do not occur South of this temperature limit. Although *S. hirundo* occurs in North America south of the temperature limit mentioned, this does not invalidate the principle elucidated by Stresemann. Concerning the whalebone whales, we may here assume a relatively high degree of adaptation to the temperature of the surface water which I am not inclined to accept in regard to these species of *Sterna*. The whalebone whales probably have a greater capability of registering the temperature changes of the water than *Sterna*. I am inclined to feel that this discussion on the relation of the distribution of the 4 species of *Sterna* to the surface water hydrography of the oceans shows to some extent that the birds associated with these oceans give indications on the quality of the water. Murphy states that one of the primary purposes of his book lies in the fact that it will show that the easily observed birds "offer a ready key to many characteristics of the ocean water and of its hidden life." In this connection, he continues and states: "the correlations are still very imperfectly worked out and yet a single specimen of an oceanic bird from a remote and little known island is, in some cases, sufficient to give a broad clue to the character of the surface water in the vicinity and the kinds of organisms that inhabit it. Furthermore, as we shall see in connection with studies made at the northern limit of the Humboldt Current, birds are sensitively adjusted and quickly respond to periodic changes in the character of the surface water. In the retreat of certain groups of birds from an area that has formed part of their ranges and the invasion of the same region by other species from a different maritime life zone, we can sometimes see a reflection of what is simultaneously occurring in the way of actual replacement of one kind of surface water by another."

IV. The Migrations of *Sterna Macrura*

The very long migrations undertaken by *S. macrura* each year have already been described above. An attempt has been made to explain the migratory path of the North American coastal sea swallows on the assumption that this path is formed by the ancient path of immigration to North America. However, it is scarcely an explanation to qualify the path of migratory birds as a path of immigration. The selection of a path of immigration has causes which should also be made clear. However, we are here on uncertain ground. A bird in the process of migration is subject to the influence of ecological factors quite as much as during the sedentary periods of the life cycle. For such an exhausting trip as that made by *S. macrura*, the muscular effort requires an ample supply of suitable food. Observations on the biology of migration of North American species of birds do show that the procurement of food along the path of migration is of importance and examples can be cited that birds select their path precisely over the environment which is able to afford the suitable food which is of different types and grades as a function of the nutritional predilections of a species. Obviously, the bird attempts during migration to satisfy purely instinctively the ecological demands as well as possible. On the other hand, there are species which can fly long

distances without requiring any food. It has been determined that *Pluvialis dominica* first procures a reserve of food before attempting the long trip across the Atlantic Ocean to South America or from Alaska to Hawaii. The nutritional basis of *S. macrura* is in the sea and its procurement of food must take place during the actual migration. However, Wynne-Edwards (1935) observed that *S. macrura* apparently gathers food from the surface of the water only infrequently during migration from North America to Europe. However, on this migration, *S. macrura* has to cross in part water of the Gulf Stream and of the Atlantic Current which is not so rich in food as the waters outside of New Foundland where the species has been observed to catch fish intensively. Fig. 10 clearly shows that the limit for the area of distribution of the whalebone whales in the northern Atlantic Ocean runs in a northeasterly direction and avoids the warm currents of this ocean. Not until the latitude of Iceland and Scotland does the limit mentioned curve southeast. A similar distribution is also that of *Clupea s. str.* in the Northern Atlantic Ocean (cf. Ekman 1935, p. 237). This situation would appear to indicate that the Gulf Stream and the Atlantic current in their southern section are poor in pelagic organisms suitable as food for whalebone whales and also for *S. macrura*. Not until it reaches the vicinity of the British Isles does the Atlantic Ocean become rich in plankton (Jespersen 1925). Ingebrigtsen (1929) reports that *B. musculus* occasionally migrates from the Northwestern Atlantic Ocean to the Northern Arctic and consequently also to the waters at the coast of Finnmarken by avoiding the Icelandic waters and keeping north of the Gulf Stream.

To return to the question of the path of immigration to North America of *S. macrura*, we need to find out where the species may have originated. There is an opinion that most of the now living species of birds had been developed by the end of the Tertiary Period and that, in any event, all the now existing subspecies had achieved their final form. During the Quaternary Period, mainly differentiation of race can have taken place.

Ekman (1935) is of the opinion that at least in certain parts of the Northern Pacific Ocean a temperate climate prevailed during the entire Tertiary Period which may have constituted the prerequisites for the development of the temperate-climate litoral fauna. According to this, Northeast Asia and Alaska apparently already had a temperate climate during the Eocene Period whereas the Northern Hemisphere had a warm climate. East Greenland at 69° northern latitude may have had a tropical climate similar to that of England and Central Europe during the Eocene Period.

According to Stegmann (1938), the arctic bird fauna is much too characteristic as that it could have been developed only during the Quaternary. According to Stegmann, we must assume an interval of time for the development of a new species of bird which goes back at least as far as the middle of the Tertiary Period. According to this author, several endemic species and one endemic family are found in the Arctic. From a

general viewpoint, arctic birds show the following map of distributions: the greatest number of species occur on the Chuckchee Peninsula and in Alaska and are distributed from here by a gradually decreasing number of species towards West and/or East. Stegmann is of the opinion that the recent distribution of the arctic bird fauna indicates that it was formed on that part of the Bering Land now lying below the surface of the sea, in Northeastern Siberia and in Northwestern North America. The same author also believes that we must arrive at the conclusion, on the basis of the theory of the displacement of the pole, that the parts of Asia and North America mentioned above together with the Bering Land acquired an arctic climate already during the Miocene Period.

Ekmann (1935) writes that the arctic littoral fauna has its main area in the Sea of Okhotsk and in the Bering Sea but does not believe that these areas are also the area of origin of the fauna in question. In the opinion of Ekmann, the Polar Basin must also be considered in this connection for the pre-quaternary periods. During the Quaternary, migrations of arctic species from the northern and northwestern parts of the Pacific Ocean almost certainly took place mainly in an eastern direction, according to this author. Häge (1924) stresses that at least 16 species of mollusks now living in arctic areas occurred in the northern Pacific Ocean already during the Miocene and are to be found in the northern Atlantic Ocean only during the later Pliocene and Quaternary.

The first elements of an arctic bird fauna are of American origin, according to Stegmann. The latter believes that the arctic climate became distributed eastward over the North American continent by covering Northern North America with ice during the Pliocene but not Northern Alaska and the Canadian Islands which remained free of ice. Under these circumstances, the arctic bird fauna may have become formed north of the ice barrier so that a retreat of the fauna southward could take place only with difficulty. According to Stegmann, the forms which had adapted to the arctic environment therefore became distributed in Eurasia from Northeastern Siberia westward during the Quaternary ice cover. The isolation necessary for the formation of species and race may possibly also have been intensified even further through areas with polar water not well suited for the procurement of food. Perhaps the polar-water areas were more numerous and larger during the ice periods.

Certain facts therefore seem to indicate that a temperate-climate and later arctic fauna first began to be formed somewhere in the area of the Bering Sea and of northernmost North America although it is difficult to delimit this area accurately. In the second half of the Tertiary Period is probably also located the time during which the type of the arctic fauna became formed. The assertion of Stegmann that an interval of time, beginning at least with the middle of the Tertiary Period, was required for the creation of new species is supported by palaeontological proof, according to him.

According to Stresemann, *Sterna* occurs in Europe and in North America together with *Larus* and *Stercorarius* already during the Miocene Period. The species of *Sterna* treated herein presumably became developed from a thermophile form. In connection with the climatic deterioration mentioned above, there probably took place the creation of a form adapted to a temperate climate from which *S. hirundo* and *S. macrura* have been developed. *S. hirundo* is probably older than *S. macrura*. I do not think that it is improbable that *Sterna fosteri* Nuttall came from the same root as *S. hirundo*. This species now lives mainly in the temperate zones of inland North America (Peters 1934). Not later than the beginning of the Quaternary, *S. macrura* should have been fully developed so that the species is relatively young. If *S. macrura* therefore did become formed in the then ice-free arctic Northeastern Siberia and arctic North America, Siberia, as assumed by Stegmann, must have been populated by this species and other species coming from the East and most probably from the area of the Bering Sea. Scandinavia also was entered probably from the East by *S. macrura* in post-glacial times, according to Ekmann (1922) who does not altogether exclude the possibility of immigration from the South. It is perhaps pertinent in this connection to stress that finds of *S. macrura* from the glacial period have been made in Italy (Lamprecht 1933). Since arctic North America and Northeastern Siberia are the most probable areas of formation of *S. macrura*, it may be assumed that the Northeastern part of the North American continent was populated directly from the West and not from the East over the long detour by way of Northern Eurasia. This then excludes the possibility that the migratory paths over the Atlantic Ocean could be an ancient path of immigration.

It is scarcely permissible to explain the migratory paths of the species without considering at least to some extent what caused it to become a migratory bird. At the time when *S. macrura* developed from the basic form that later became *S. hirundo*, it probably did not differ particularly in regard to ecological factors. During the progressive change of climate, two other factors presumably exercise a greater influence, i.e., temperature and daylight. After the process of adaptation to temperature had been terminated to a certain extent, the new race or species was then able to become distributed over the growing arctic and sub-arctic regions. It then must have occurred to a large extent in regions which were characterized during the summer by long days with many hours of sunshine per day. To this may have been added that the intensity of daylight is here greater because these regions consist of open and unobstructed surfaces of tundra, water, ice and snow.

The food predilection of these species of *Sterna* and their manner of its procurement do not constitute any great obstacles to life in arctic waters but *S. macrura* must presumably gradually have adapted itself to easily procurable food, i.e., primarily pelagic crustaceans, mollusks and certain insects. The difference between the present bill of fare of *S. hirundo* and *S. macrura* does testify that a certain adaptation to colder waters did take place for *S. macrura*.

We know that phytoplankton is dependent on sunlight and its production is greatest during the daylight period of the year. It follows from this that other plankton and pelagic organisms also are dependent on the changes in daylight factors during the year. The food suitable for *S. macrura* is therefore not obtainable to the same extent during the entire year and there is a lack of food in the Northernmost areas during the dark period of the year for *S. macrura*.

During the maximum extent of the glacial periods, the temperate and tropical zones were compressed and reduced from North and South. The birds did not need to migrate very far in order to find better fishing beds. The cold currents probably penetrated with greater intensity towards the equator from North and South and carried plankton with them. In the lower geographic latitudes, the days are longer during the six months of winter than in the higher latitudes which affords the birds more time for the procurement of food and this is a fact which should not be neglected. The quantity of food which a bird can ingest within a 24-hour day depends also on the amount of time available for hunting and catching food animals. It is very probable that *S. macrura* during the glacial period initially developed into a wandering or itinerant bird for the sake of procuring food. This process had probably been completed already after the first glacial period. After the ice cover began to retreat during the last glacial period, the breeding area of the species also became displaced further and further North. Simultaneously, the temperate and warm water regions began to extend towards the higher geographic latitudes. The areas of distribution of the pelagic organisms serving the species as food also became displaced further and further North. In the meantime, the possibility of procuring food increased in the new area during the daylight part of the year rather considerably by the change in daylight factors whereas the possibilities for the procurement of food during the dark period of the year became worse than at the time when the area of distribution extended further South. It is not the long nights in themselves which are dangerous but become so only in combination with very low temperatures. During periods with intense cold, *S. macrura* is probably unable, due to the long nights, to procure an amount of food sufficient through increased metabolism to compensate for the high loss of body heat.

It may perhaps be assumed that the species migrated already during the first glacial period and the winter of the Northern Hemisphere through the warm zone to the Southern Pole Zone in order to fish in the cold water of the latter during the summer of the Southern Hemisphere. When the last of the ice began to melt and the climate improved, the area of warm water increased to its present extent. Those areas became greater in which the food suitable for and preferred by *S. macrura* did not occur and an unserviceable climate prevailed. The darkness in the North during the winter continued to force it to wander or vagabond. Because of hydrological changes, it became more difficult in the meantime to find suitable feeding areas further southward. This time must have been a critical stage in the life of the species. Cold currents with suitable food still existed

and began to assume their present distribution and *S. macrura* had to adapt its itinerant life during the winter at that time to these regions of water.

In regard to the biology of migration, *S. macrura* shows indications that it could be numbered among the so-called instinctive migrators. It may be assumed that the habit of wandering was deeply rooted. It is difficult to decide how much time is required for such a complicated "habit" to turn into a hereditary factor but we may perhaps assume, in regard to *S. macrura*, when we consider its enormous area of distribution and its great numbers within the northern breeding areas, that this process may already have been completed during the first glacial period. If *S. macrura* or the basic form of the species closest to it, had existed already as far north as at present prior to the glacial period, then the wandering or migratory habits must probably have been formed already then because of the changes in the length of the day occurring in these regions during the year. It may certainly be assumed that the adoption of the gigantic migratory paths across the Atlantic Ocean and along its Eastern coasts by the species must have taken place by a long process of selection.

The present migratory paths of *S. macrura* across the Atlantic Ocean do cover, however, a watery region of a definite hydrological character. A comparison between Fig. 3 and Figs. 10, 11, 12 shows that the surface water in the migratory paths of the species along the west coast of Europe and Africa shows a salinity of a maximum of 3.5% in an almost unbroken belt or region and has a color shading more or less perceptibly into yellow as well as a relatively low temperature which is caused partly through cold currents from higher latitudes and partly by ascending cold depth currents. We may conclude from all this that the surface water in this eastern littoral zone of the Atlantic Ocean has much less the character of "warm" water even within the subtropical-tropical zone than the surface water along the Atlantic coasts of the two American continents. On the west side of the Atlantic Ocean, warm surface water flows towards the continents and extends far to the North and South. On the east side, the warm water on the surface is displaced by cold currents from the North and South (Canaries and/or Benguela Current) and there also occur ascending cold deep waters along a very large part of the west coast of Africa (Fig. 10). It is notable that such ascending cold water also occurs beyond the coast of the Bay of Guinea in a purely tropical surface water region.

Concerning the littoral fauna, Ekmann states (1935, p. 88): "It is no wonder then that the transition from the tropical to the temperate fauna is not very well defined in these regions. In no other region of the world is the limit of the two faunae so vague as here." Along the west coast of Africa, there are also several regions rich in nanoplankton which were investigated by Hentschel (1928, 1933). The distribution of plankton is shown in Figs. 14-16. If we compare the distribution of plankton with that of the phosphatides in depths to 50 m (Fig. 13), we

then obtain a striking coincidence. Similarly, we find that the distribution of food stuffs and plankton shows a high dependence on the currents (cf. Hentschel 1933). The area of tropical surface water forms an approximate triangle in the Atlantic Ocean and its long base stretches from the Atlantic coast of the Florida Peninsula to Porto Alegre on the Brazilian coast at about 18° Southern latitude whereas the truncated apex lies on the coast of Africa and stretches from the coast just south of the mouth of the Gambia as far as just north of the mouth of the Congo. The gigantic aggregation of warm water caused by the equatorial currents in the western coastal regions of the Atlantic Ocean and the absence of cold currents and ascending deep water within the area from Cape Hatteras to Cape San Roque are certainly the most important reasons for the poverty of plankton in these waters. In the Northern South American coastal waters, production of plankton may also be hindered perhaps through the high turbidity from the mud carried by the rivers. The mud is transported by the equatorial current from the mouth of the Amazon River northwestward along the coast as far as the eastern coastal regions of Venezuela and many rivers continually add to it along this path.

The lack of suitable food both in qualitative and in quantitative respect would seem to be the most important reason why *S. macrura* does not migrate along the tropical east coast of America. It is possible to suggest other reasons as well. Each species of bird probably possesses definite habitat requirements, the realization of which is necessary for the well-being and consequently breeding of the species. The habitat requirements of *S. macrura* consist in extensive, very uniform coastal areas of mountainous or sandy character and poor in high-growing vegetation. Similar viewpoints are also developed by Palmgren (1938). The American coastal regions in general do not correspond to these requirements whereas the western coastal areas of Europe and Africa agree better with them. It may be suspected that the migratory paths are also based to a certain extent on the realization of habitat requirements and in that case, the migratory paths of *S. macrura* along the eastern coastal region of the Atlantic Ocean become more understandable because these areas in the subtropical-tropical region have a greater number of features in common with the breeding and wintering areas of the species than those in the West.

The birds are probably able to recognize certain air masses and typical wind directions which is also assumed by Griffin (1944). Included in the habitat requirements are probably also the different characteristics of the air.

The apparently unexplainable ability for orientation which *S. macrura* must possess is illustrated, by the theoretical and actual prerequisites exposed in this report, in a manner which permits a logical explanation. In this connection, it seems to me most natural to derive the explanation for the ability of orientation (and consequently the ability

to keep to the migratory paths) on the explanation given by Griffin for the general ability of orientation of birds which he summarizes as follows: "The combined use of familiar landmarks together with simple geographical, meteorological and ecological relationships such as those described above, seems more reasonable as an explanation of migration and homing than the postulation of a new sense organ" (cf. Pearse 1939). *S. macrura* then does not possess a true long-distance orientation but rather a step-by-step or, more accurately, a progressive orientation. We must also presuppose a well developed memory and primarily a memory for change in direction which is perhaps possessed by all mammals and birds but which is especially well developed in certain species. Leading ornithologists (cf. Ising 1945) today no longer believe in a special sensory organ of orientation.

We see already from the distribution of the whalebone whales (Fig. 10, 12) that the hydrological factors on the two coasts of the Atlantic Ocean are different. Moreover, Hentschel (1933), pp. 146-150) shows the enormous difference in quantitative respect between the east and the west coast of the southern Atlantic Ocean in regard to metazoan plankton as well as nannoplankton but the qualitative difference is insignificant. For the whalebone whales, the existence of specific food in the water is of great significance because they depend in part on exactly the same food animals as *S. macrura* and *S. vittata* so that we can make a comparison through wholly natural reasons with the specific migratory path of *S. macrura* along the east coast of the Atlantic Ocean. In my opinion, it is based in principle on the same autoecological factors as the distribution of the whalebone whales along the west coast of Africa. I also refer to the observations according to which *S. macrura* does not migrate along the west coast of Europe without interruption but stops on its trip south at points where food is abundant.

The American coastal waters of the tropical zone are poor in plankton and the number of finds of whalebone whales outside of the actual areas of distribution is few so that the autoecological relationship is unsuitable for *S. macrura*. To this we should add that probably the climatic conditions are less suitable than along the west coast of Europe and Africa.

It remains to cover in a few words the peculiar migratory movements which have been noted in the southern Atlantic Ocean (Lincoln). The path of *S. macrura* from the southwest coast of Africa curves southwest and then turns northwest in certain cases. In many cases, this is certainly mere wandering in the wintering area and a glance at Fig. 10, 11, 12 will show us that the species here flies over the cold water zone which obtains its surface water from the Benguela Current, the West-Wind drift and the Falkland Current. The flight paths of the species in the southern Atlantic Ocean therefore seem understandable both from climatic as well as from autoecological viewpoints.

In the Pacific Ocean, the migratory path along the west coast of North America is more suitable from hydrological and autecological standpoints than along the east coast of Asia which moreover has not been observed. The migratory path by way of Tobolsk-Black Sea-Mediterranean outlined earlier has not been definitely determined but is not altogether improbable on the basis of observations and finds. Insofar as west Siberian birds do not migrate exclusively along the Polar sea coasts of Siberia and Russia but follow a southern path across the continent, the migratory path indicated (on page 18 of original) is probably the most suitable. Migration along the coast of the Indian Ocean has so far never been observed.

It would seem that *S. macrura* leaves the southern parts of the breeding area earlier than the northern parts. Witherby mentions that the English breeding places become abandoned toward the middle or end of August and that transit continues until the end of October (cf. Palmen 1887, p. 349). This may be connected with the fact that the temperature of the surface water within the southern parts of the breeding area rises so high during the late summer that changes occur in the pelagic fauna of the surface water which deprive the species of proper food whereas the hydrological factors in the subarctic and arctic parts remain more favorable during this time. The phenology of *S. macrura* in certain areas has probably developed in an interrelation with that of the euphausiaceans. The times of arrival of the species in Norwegian waters coincide quite well with the beginning of the spawning period of *Meganyctiphanes norvegicus* (Norwegian west coast in the region of Møre) and of *Thysanoessa inermis* (Finnmarken waters). Departure takes place at the end of July and continues through August and during this time the volume of pelagic organisms is also reduced. There are data on an occasional early arrival of *S. macrura* (beginning of May and/or end of April) from Iceland and the Davis Straits. This may be connected with a good food supply already occurring in these waters during spring. Ingebrigtsen (1929) also mentions that *B. musculus* arrives earlier in the waters of Iceland than in those of Finnmarken, i.e., end of March and Beginning of April. This is probably connected with the fact that the production of species of *Thysanoessa* manifests itself early in these waters.

The assumption that the migratory path of *S. macrura* from and to eastern North America constitutes an earlier path of immigration of the species is not in agreement with the viewpoints exposed in this report in the attempt to interpret the distribution and the selection of migratory paths by the species. We should remember that the path of immigration of a bird species (or any other species of animal) into a certain area must be ecologically suitable for the species. The occupation of a new area takes place gradually and the most appropriate paths may not be found immediately. If the species is a regular migrator, it may perhaps utilize the old paths of immigration for migration as long as they are ecologically suitable or until more appropriate directions from ecological viewpoints are discovered. There are examples for changes in migratory paths as well

as examples, as stressed by Franz (1943) that such changes have been due to action by man. In other cases, some species of birds have abandoned the habit of migration under human influence but such cases probably do not concern true instinctive migrators. Franz stresses that the present-day migration of some species is "in no respect" conclusively demonstrable as based in the past, e.g. glacial period. This is probably a somewhat too all-inclusive point of view but it does seem reasonable to state that the path of immigration of a migratory species of bird is probably used as path of travel as long as it remains ecologically suitable.

In this connection, we also want to expose some summary viewpoints on the occurrence of *S. macrura* South of the sub-arctic region, i.e., on the south coast of the North Sea, on the east coast of North America south of Newfoundland, and on the northwest coast of North America. We know that the inland ice had its greatest extent in North America and there was a large unbroken glacial region also in Europe. On the other hand, it is usually assumed that the greater part of the present-day Arctic Asia was free of ice, including the shores of the Bering Sea and of the Sea of Okhotsk. However, we know little of the extent of the glacial cover north of Asia and assumptions seem to differ greatly (cf. Antevs 1929 and Stedmann 1938, p. 100). Prior to the greatest extent of the ice cover, *S. macrura* probably occupied the regions mentioned at the beginning of this paragraph where an arctic and subarctic climate prevailed. Where the ice extended furthest south, *S. macrura* was forced to wander further South. That the species then remained relatively far southward in the coastal areas mentioned, in spite of the climatic change, is certainly connected with the fact that the hydrological factors along these coastal stretches retained a more northern character, due to surface-current and depth conditions, than is normal for surface water in these latitudes. Hydrological together with depth conditions consequently favored the prerequisites of the biology of nutrition for the species so that it remained in relatively southern geographic latitudes. We might recall here that these waters contain abundant high-sea fishing beds. In my opinion, there are reasons why *S. macrura* in these areas and in the Baltic Sea may be regarded as a relic of the last glacial period as well as of the time of the Yoldia Sea and perhaps also of the Baltic Glacial Sea. If we take into account that *S. macrura* is able to breed as far toward the North Pole as indicated (on p. 10 of original), it is very probable that the species was also able to breed on the ice-free coastal stretches of the glacial regions. The species has consequently perhaps been able to retain the area of distribution previously possessed after the last glacial period, e.g. along the northwest coasts of Europe. Even though the first settlement of the species in northwestern Europe may have taken place once long ago from the Northeast, we may imagine that the present occurrence on the North Sea may also be derived in part from a re-immigration from the South and in part perhaps also from an immigration of individuals from the ice-free regions on the Norwegian coast. It is therefore possible that the migratory paths for the birds of the North Sea region are constituted

in part by paths of immigration subsequent to the last and the immediately preceding glacial period. We may also suspect a distribution from Siberia toward the West, also subsequent to the last glacial period. In the Bering Sea and on the north coast of Alaska, it was possible for the species to find breeding areas even during the height of the glacial period. Moreover, in view of the exceptional endurance in flying of *S. macrura*, immigration to the southern shores of the North Sea and the west coast of Norway from the three areas mentioned, after the last and the immediately preceding glacial period, is in my opinion highly possible.

Concerning distribution and the immigration and migratory paths of *S. macrura*, all are based primarily on climatic and hydrological factors. The most important of these factors for present-day distribution would seem to be at least in certain cases the hydrological factor but we must assume that the ecological reaction of the species was based from the start on a certain adaptation to climate and certain food predilections.

The analysis of distribution and migration of *S. macrura* here made shows that a body of water with certain hydrological characteristics can have an influence as concerns the selection of migratory paths and breeding areas on a bird species which is dependent for food on certain aquatic organisms.

V. Some General Ecological Viewpoints

The euphausiaceans, the larvae of *munda* and the pteropods form a group of organisms with a certain ecological unity or interdependence. Their relation to environmental factors is rather similar and they are utilized as food by certain organisms. Among those preying on them are particularly *Mystacoceti*, *Sterna* and certain fishes, e.g. *Clupea* and *Mallotus villosus*. The two groups therefore have a relationship of exploiter and exploited in the ecological meaning. It would be possible to say that they form the biotic part of an ecological complex in which the pelagic vertebrates constitute the center of gravity. Since the euphausiaceans are decidedly the most important, this ecological complex might be designated as a euphausiacean complex. Since the occurrence of the vertebrates as well as their distribution and phenology is dependent on definite abiotic and biotic hydrographic factors, the entire ecological complex is dependent on these and consequently also on other factors which regulate and influence the hydrographic factors. Such an ecological complex necessarily acquires a certain delimited geographic distribution. Study of such ecological complexes must consequently be an aid in the comprehension of the spatial distribution and displacement of the organisms.

An ecological complex consists of two parts, a biotic and an abiotic part (cf. Eidmann 1942: abiotic and biotic complex). If one single link in the ecological complex becomes lost, all the adjacent links of the complex are also destroyed.

VI. The Taxonomic Position of the Four Species of Sterna

A theory has been presented above according to which *S. macrura* and *S. hirundo* are closely related and originated from a common basic form. Below are listed some observations which support my opinion on the close relation of the two species. We begin with a discussion of the relation of the two southern species to the two northern species.

The special chapter will have shown that morphologically *S. hirundinacea* is closer to *S. hirundo* whereas *S. vittata* is more closely allied to *S. macrura*. From ecological viewpoints, however, *S. hirundinacea* was seen to have a closer relation to *S. vittata* and *S. macrura* than to *S. hirundo*.

Murphy establishes a brief comparison between the different groups of Laridae on the Northern and Southern Hemisphere, without entering in detail on the taxonomic position of the individual species. It is of course rather difficult to treat these questions other than merely speculatively as long as no genetic investigations have been carried out. Comparative points in regard to morphology and ecology are able, however, to furnish certain guide lines. Concerning Laridae, Murphy writes that it is "quite possible that South America is the last stronghold par excellence of certain "living fossils" which during long ages have been pushed out from the Northern land areas towards the periphery of the world." However, *S. hirundinacea* and *S. vittata* can hardly be counted among the living fossils. Because of its peculiar adaptation to environment, *S. hirundinacea* may be older than *S. vittata* on the Southern Hemisphere.

The great similarity between *S. macrura* and *S. vittata* is stressed by Murphy. He writes that *S. vittata*, "appears to be, indeed, so closely allied to *Sterna paradisaea* that one may conceivably have originally been derived from the other." It does seem to me as if the relation between the two species could be clarified in detail with the aid of what has been said earlier in this report on their living conditions and the development of the present-day species of *Sterna*. Murphy apparently also assumes, that the development of the family *Sterna* took place on the Northern Hemisphere. Morphological reasons support the assumption that *S. vittata* originated out of *S. macrura*. There is also biological support for such an assumption which is that *S. macrura* in migration stays precisely in the areas during the southern summer where *S. vittata* now breeds. In my opinion, contingents of *S. macrura* remained originally and changed their habits by breeding during the Southern summer. *S. vittata* then originated from these populations. We know of several bird species that individuals may stop breeding and vagabond in the wintering area or along the migratory paths. There are also bird species with migrating and with non-migrating races. The assumption that *S. vittata* originated from *S. macrura* in the manner just outlined becomes even more probable by

reference to a similar process of separation which has taken place in our time: *Ciconia nigra* has recently become sedentary and is breeding in South Africa.

What was the reason for which *S. macrura* remained in the South? The most valid explanation probably lies in the similarities of climate and food supply between the old breeding and the wintering area. To this is added the circumstance that the occurrence of plankton and pelagic crustaceans is greater in Southern than in Northern seas. The ecological bases for successful resettlement consequently were good. The necessary change in the period of propagation is not particularly astonishing because such phenomena have long been known for birds as well as for mammals. One example has already been cited in this report, i.e., *S. hirundinacea* which possesses different breeding periods in the North than in the South of its area of distribution.

It is assumed that *S. vittata* is a species different from *S. macrura* but actual proof for the existence of a true difference in species does not exist. In my opinion, there are scarcely any obstacles to the assumption on a morphological and biological basis that we are confronted by different races of the same family.

However, certain differences in regard to manner of life do exist for *S. vittata* in relation to *S. macrura*. *S. vittata* does not seem to be a migratory bird. The indications on the occurrence of the species outside of the breeding periods are very uncertain. It does not seem to remain during the winter in the Southern Orkney and the Peterman Islands but occurs also during the winter in South Georgia, according to Lönnerberg (1906). The case may be that the species concentrates on certain locations and areas more favorable for the procurement of food during winter, e.g. open water and areas where the day is longer than in the true antarctic region but it usually does not occur north of the sub-antarctic surface-water zone, according to all available information. It may have been the more abundant existence of food in the Southern seas which persuaded *S. vittata* to abandon its migratory habits which originally were probably hereditary in this bird.

Another difference in comparison with *S. macrura* is their low resistance to wind. It may sound peculiar that a sea swallow from the stormy southern seas would not be specially resistant to wind but there are certain observations which support such a statement. Murphy never observed any individuals of *S. vittata* in South Georgia at a distance of 25 km or more from the coast. "For such reasons, it seems probable that the tern is sedentary and not given to long flights across the ocean either in search of food or in migration. Like other members of its species, it avoids contests with the raging gales of the Far South" as stated by Murphy in regard to *S. vittata* in South Georgia. It has also been observed that the bird attempts to dig small holes in the sand for protection from the wind at the "first gusts of blizzards and williwaws."

Except on the Antarctic continent, the breeding areas within the antarctic and subantarctic region are very limited and far distant from each other. Because the species seems to be rather stable in the sub-antarctic zone, the separation of the colonies on the different island groups is all the more marked. The lesser resistance to wind of *S. vittata* as compared to *S. macrura* contributes probably also to isolate the colonies. The greater sedentary habits of the species as well as its lesser resistance to wind are probably related to the occurrence of food around the areas of settlement. When we consider the isolation existing between the highly restricted breeding areas of the species in the sub-antarctic zone, the subdivision of the species into races existing in this zone becomes more easily understandable. This may be an application of the so-called Sewal-Wright effect. By way of comparison we can point out that *S. hirundinacea* occupying an unbroken breeding area reaching from Tierra del Fuego into the tropical zone, does not appear to be subdivided into races. At the earliest, the origin of *S. vittata* can be traced back to the first glacial period and possibly only to the most intensive period. We might therefore here speak of a case in which a chronological estimate of the formation of the race would be possible. In any case, *S. vittata* must probably be regarded as a young form.

It is not improbable that *S. virgata* also originated out of *S. macrura*. Its great similarity to both *S. macrura* and *S. vittata* has been stressed. Concerning the manner of life, there also appear to exist similarities with *S. vittata*. It may also be suspected that *S. albistriata* has a similar history of development as *S. vittata*. Its manner of life seems to resemble more that of *S. hirundo*, according to Alexander. There is also a suspicion that the position of the three sea swallows of the Southern Seas as independent species has not yet been fully clarified in their mutual relation and has apparently not yet been investigated with sufficient accuracy. We discussed in the special chapter the difficulties in distinguishing between *S. macrura* and *S. hirundo*. Many of the characteristics indicated by the researchers are not entirely reliable. In several cases, the determination of species may therefore depend perhaps on only one single "distinctive" feature. This type of procedure is not correct, especially since we have no insight into the genetic relations. The circumstance that characteristics vary greatly and are often difficult to assign to a definite form among two closely related forms may be proof that a real difference of species does not exist and that bastardization occurs.

I made observations on the Swedish West coast which may indicate that bastardization may occur between *S. hirundo* and *S. macrura*. At the biological station of Klubban at the mouth of the Gullmar Fjord, I observed, three summers in succession, a pair of sea swallows in which the male was a typical *S. hirundo* and the female showed a very pronounced type of *S. macrura*. It was possible to approach the birds very closely and I always utilized for observation my binoculars (10 x 45). Copulation was observed and I saw the birds carry food to the young. I did not find

the nest. The female was such a pronounced type of *S. macrura* that, although I did not kill and examine it, I am of the opinion that it was a true *S. macrura*. In order to see clear in regard to the relation between *S. hirundo* and *S. macrura*, a large number of individuals from colonies with both species must be investigated and compared with individuals from areas in which only one of the two species occurs.

In summation, I want to present my viewpoints in regard to the mutual taxonomic position of the four species of *Sterna* treated in this report as follows. *S. hirundinacea* was the first to become separated from *S. hirundo* or its immediate predecessor. After the onset of arctic and sub-arctic climate on the Northern Hemisphere, *S. macrura* gradually developed from the basic form shared with *S. hirundo* which was adapted to a temperate climate. Perhaps because of the seasonal variations in daylight and the changes in the occurrence of certain pelagic crustaceans and mollusks in the Far North, *S. macrura*, originally probably highly adapted to a sub-arctic and arctic climate, assumed migratory habits which led it into parts of the Southern Hemisphere geomorphologically, climatologically, hydrologically and alimentarily corresponding to the area of development and breeding on the Northern Hemisphere. This probably took place by reason of the more favorable alimentary conditions in the Southern seas which induced certain individuals of *S. macrura* to settle and breed in the South. *S. vittata* and probably also *S. virgata* is descended from such individuals of *S. macrura*.

Summary

This paper deals with the distribution and migrations of *Sterna hirundo*, *S. macrura*, *S. hirundinacea* and *S. vittata*. Primary importance is attached to the distribution and migration routes of *S. macrura*.

The recent distribution of these *Sterna*-species is seen from the point of view of nourishment, climatological and hydrological factors nowadays and during the quaternary glaciation. *S. hirundo* and *S. macrura* seem to have developed from the same origin. The former is adapted to temperate climate and the latter to arctic and subarctic climate. *S. macrura* is a coastliving bird though in subarctic and arctic territories also breeding at fresh-water. Its food consists mainly of pelagic crustaceans (*Euphausiids* a.o.) and molluscs, at fresh-water in North Europe nearly exclusively of insects. In the Baltic Sea *S. macrura* feeds on insects, Baltic herring and sticklebacks. The breeding and winter territories of *S. macrura* are to be found at oceanic waters rich in nanoplankton (and as a consequence metazoa-plankton). Probably *S. macrura* has developed in the old Bering country and northwesterly North America and from there spread to eastern North America and northern Eurasia, i.e. in two main directions. So it was adapted to the long days of the arctic summer but was forced to go to the south during the dark northern winter in order to obtain the sufficient food quantities, and *S. macrura* became a migratory bird. Very soon it was adapted to the pelagic crustaceans

and molluscs of the arctic and subarctic waters and the migration routes were laid over waters with rich plankton production. The recent migration routes (Fig. 3) run over cold or relatively cold waters (cold streams, upwelling water) with high production of certain plankton organisms (Fig. 10, 14, 16). *S. macrura* seems to avoid warm waters during both the breeding period and winter and as much as possible during the migration. *S. macrura* seems to be bound to open country during the breeding season and probably a "habitat-schema" has an influence even upon the choice of winter territories and migration routes. The distribution during the breeding season, winter and the migrations is compared with the distribution of the *Mystacoceti*-species; similar food (Fig. 12). It is possible that *S. vittata* has developed from populations of *S. macrura* remaining in the antarctic and subantarctic waters during the northern summer. As one cause of the suspension of the migration back to the northern breeding territories one can point out the very rich plankton life in the surface water of the southern cold oceans. *S. macrura* is distributed continuously circumpolar and is not divided into races. It is not known from the eastern Asiatic coast south of the Tchuktch Peninsula and at the sea of Okhotsk. I think this depends on inconvenient hydrological relations and to some extent on the great frequency of fog. There are reasons for speaking about a law of the least ecological resistance.

At the antarctic and subantarctic islands well isolated populations of *S. vittata* have settled down and in that way geographical races are developed.

For three years I have observed on the western Swedish coast a couple of *Sterna*, the male being a *S. hirundo* and the female a *S. macrura*. I saw them copulating and in courtship and I also saw them gathering food. Probably it was the same couple all the three years. These observations perhaps favour the belief that the speciation is not finished yet.

FIGURE CAPTIONS

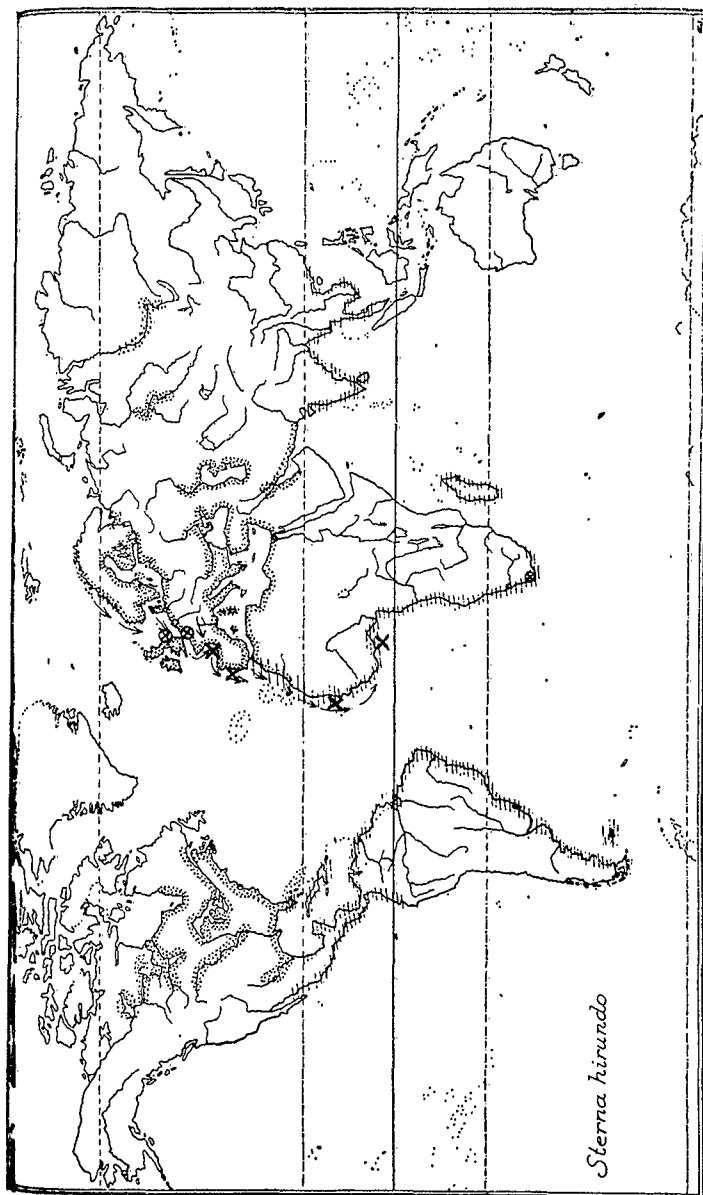


Figure 1. The distribution of *Sterna h. hirundo*. The dots indicate breeding areas, the lines the wintering areas, and the arrows indicate the migratory paths of the European birds. A circle enclosing a cross identifies finds of ringed Swedish birds and a simple cross ringed English birds.

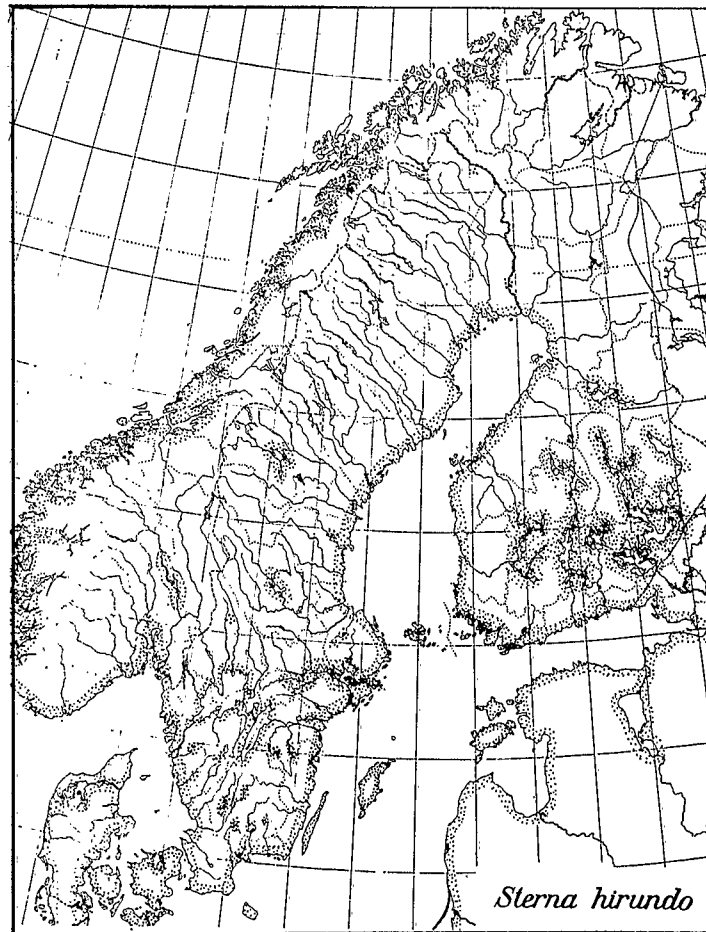


Figure 2. The distribution of *Sterna hirundo* in the Nordic countries.

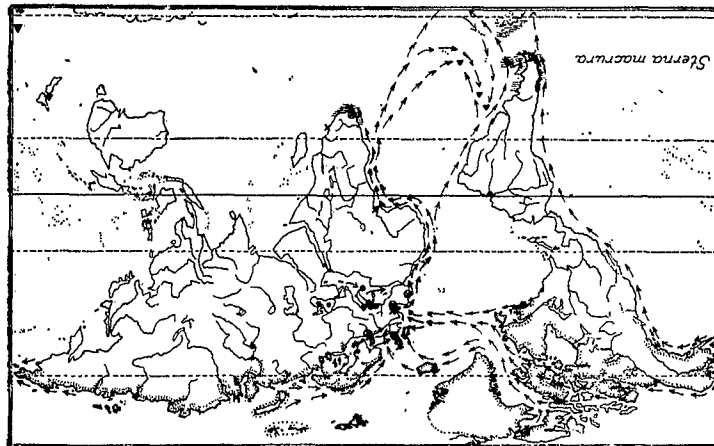


Figure 3. The distribution of *Sterna macrura*. The dots indicate the breeding area, the lines the wintering area, and the arrows indicate the migratory paths of the birds from the breeding to the wintering areas. Solid squares indicate bird-ringing stations, solid triangles indicate finds of wintering birds in the Southern Atlantic Ocean and solid circles finds of itinerant birds. A circle enclosing a cross designates finds of ringed Swedish birds and a simple cross finds of ringed North American birds. (Map based in part on Lincoln).

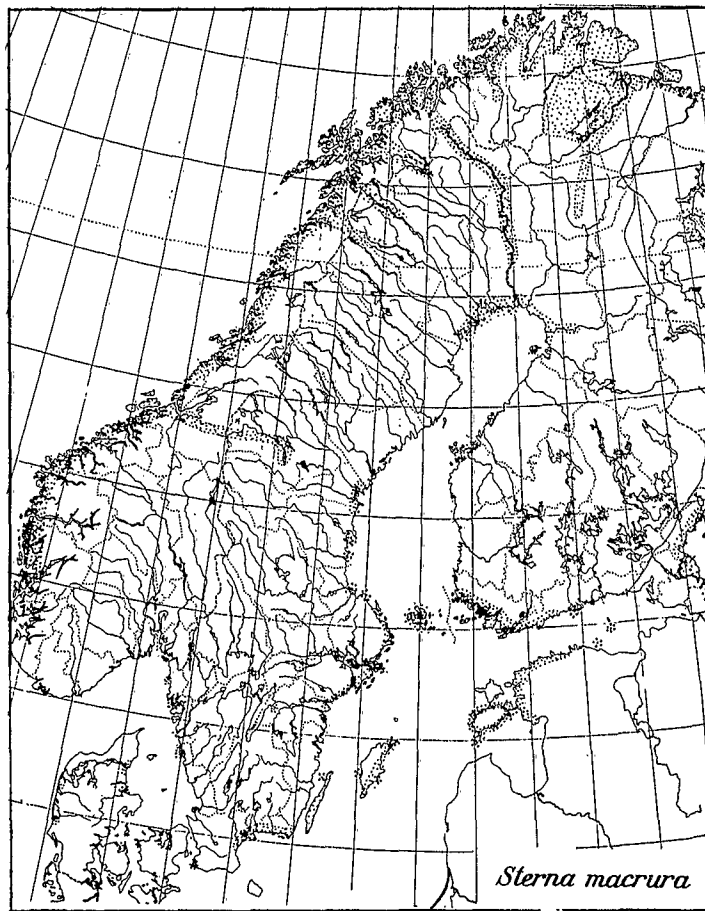


Figure 4. The distribution of *Sterna macrura* in Nordic countries.

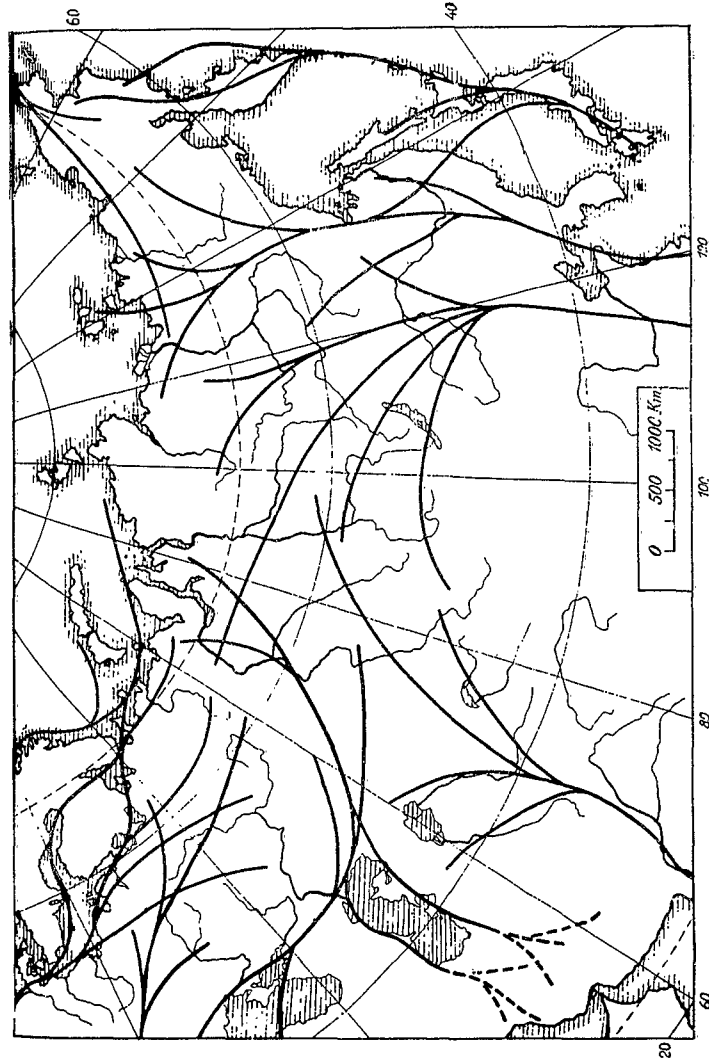


Figure 5. Directions of migration in Northern Eurasia (from Dementjev, p. 484).

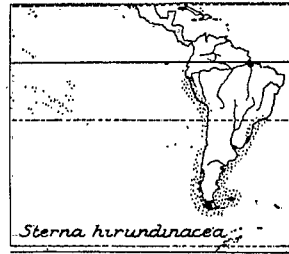


Figure 6. The distribution of *Sterna hirundinacea*.

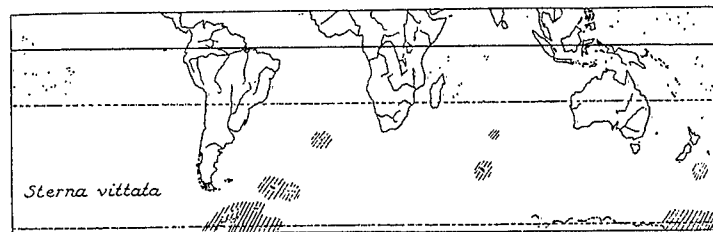


Figure 7. The distribution of *Sterna vittata*.

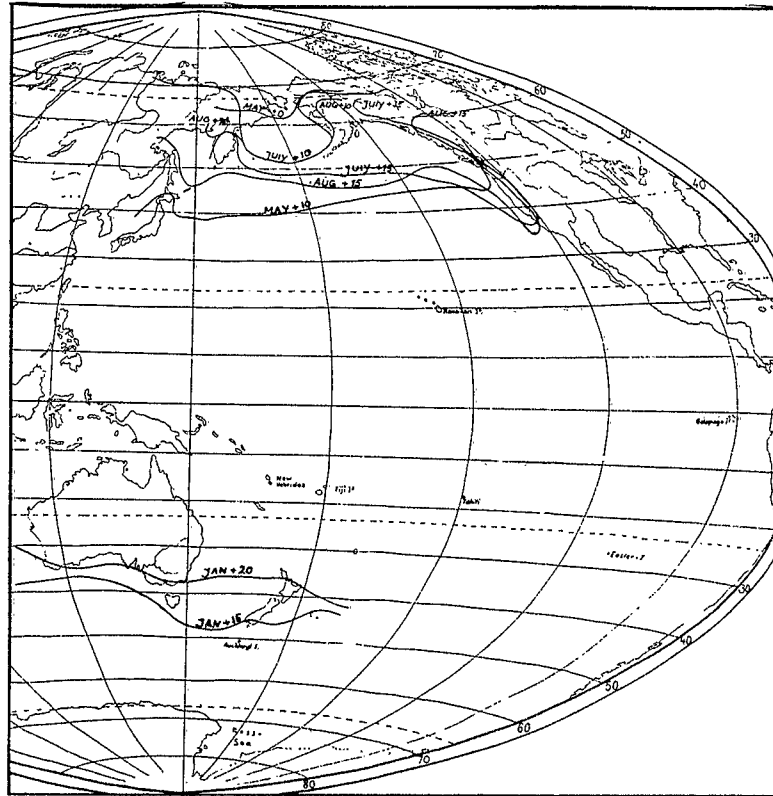


Figure 9. Isotherms of the air at sea level in Pacific Ocean

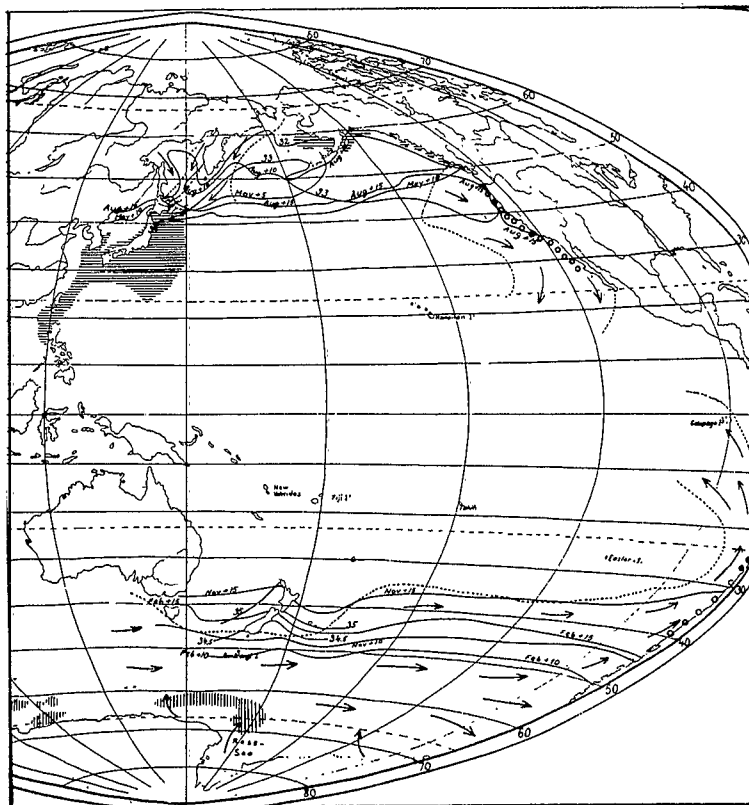
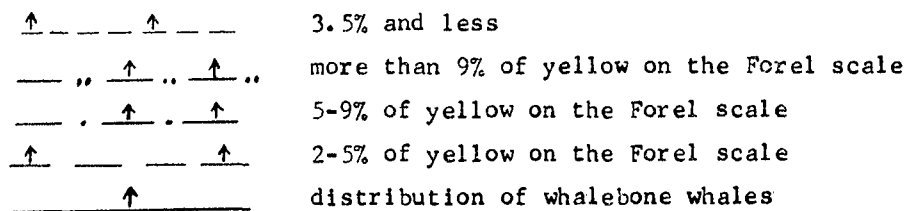
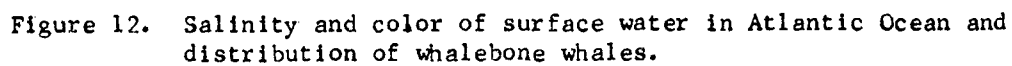


Figure 11. Surface-water isotherms and isohalsines in the Pacific Ocean. Arrows indicate the direction of flow of cold surface water. Thinly drawn lines delineate regions with cold surface water or currents. Horizontal shading identifies high-sea fishing beds and perpendicular shading the hunting areas for blue whales. Small circles designate ascending cold deep-water currents.



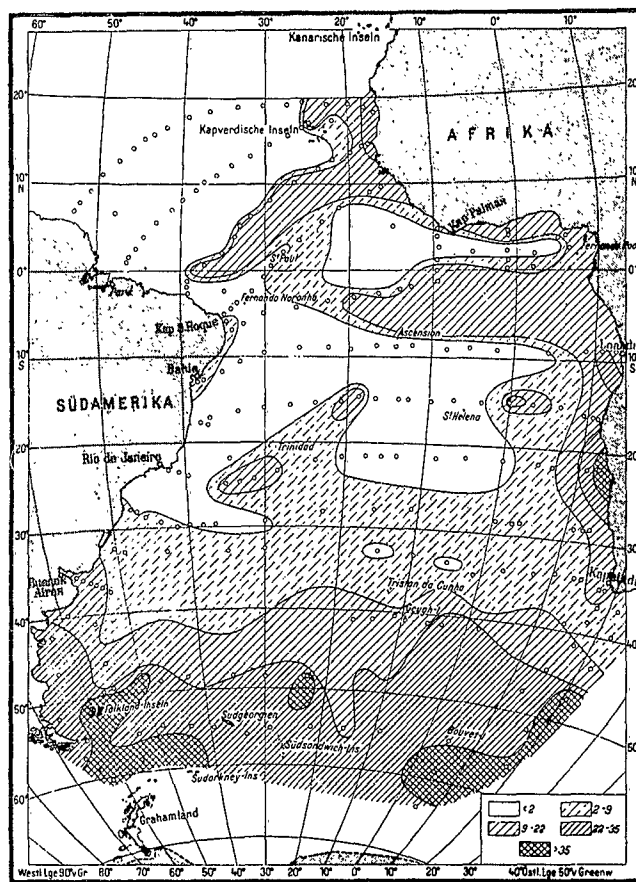


Figure 13. Phosphate content within depths to 50 m of Southern Atlantic Ocean (from Hentschel 1933).

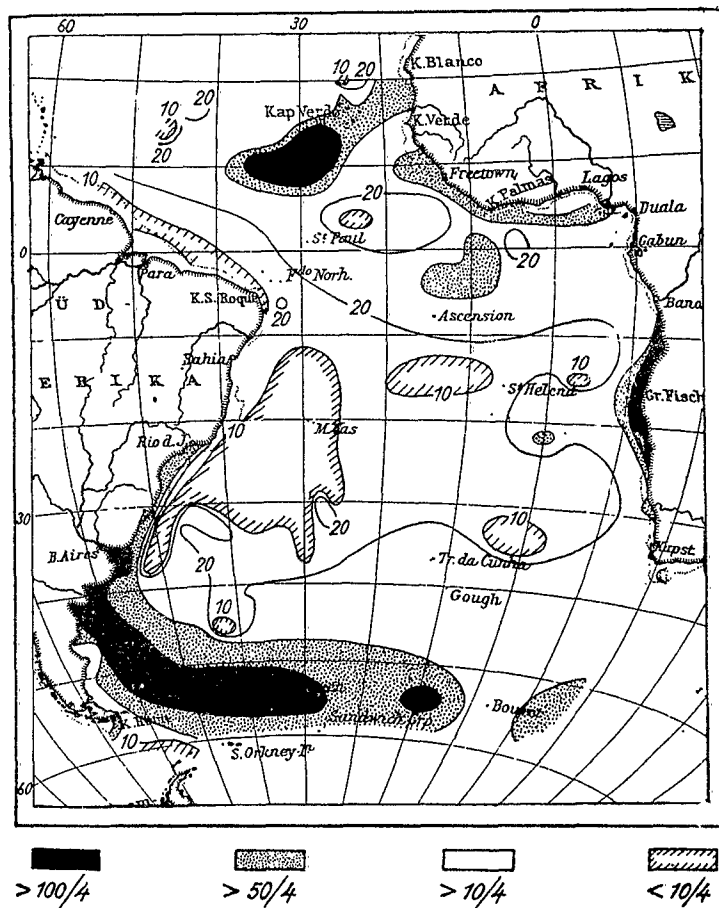


Figure 16. Metazooplankton in Southern Atlantic Ocean in organisms /4 lit. (Hentschel 1943).

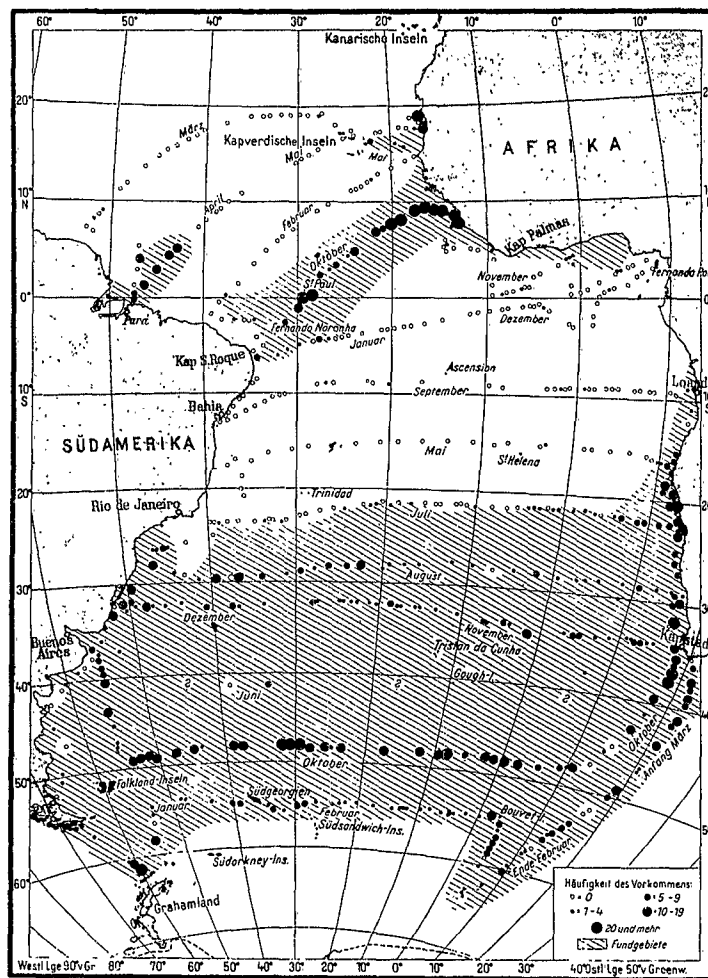


Figure 17. Frequency of the birds in Southern Atlantic Ocean behind the "Meteor" according to term observations. The shaded areas indicate regions where accompanying birds occurred regularly (from Hentschel 1933).

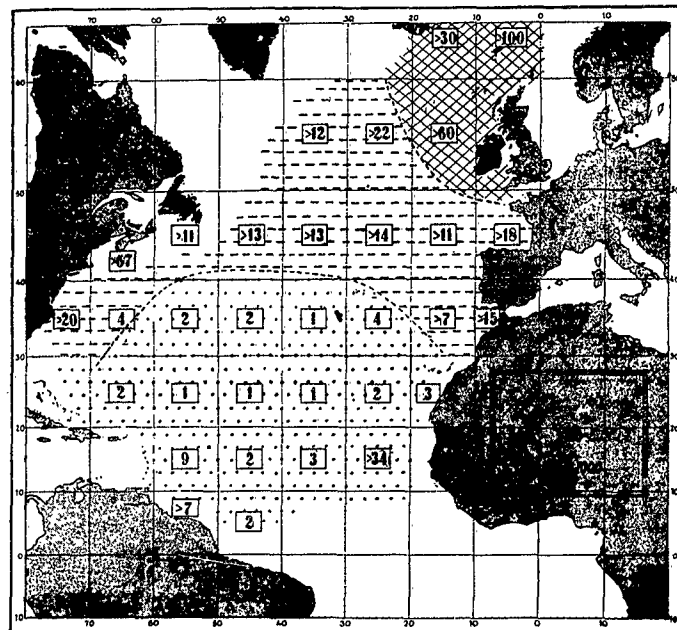


Figure 18. The distribution of amounts of plankton and average number of birds observed within one day in the Northern Atlantic Ocean. The amounts of plankton indicated are based on the amounts caught in the upper layers of water during a period of one hour (from Jespersen 1925).

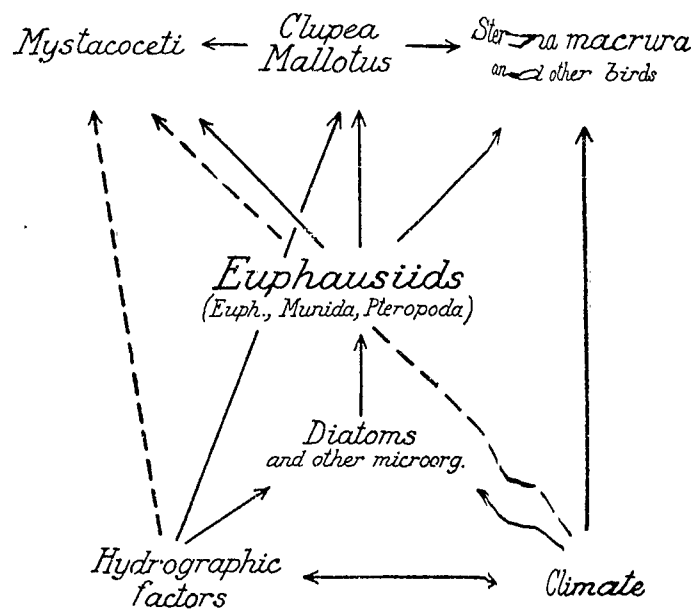


Figure 19. Ecological diagram.